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Plant species diversity and composition in limestone forests of the Vietnamese Cat Ba National Park

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Abstract

Plant species diversity and composition play crucial roles in many ecosystem services and are largely influenced by environmental conditions, as well as natural and/or anthropogenic disturbances. However, our knowledge of the drivers of plant species diversity and composition in the limestone forests of Vietnam, a hotspot of biodiversity, is limited. To fill this knowledge gap, we surveyed plant species in the Cat Ba National Park (CBNP), located on a limestone archipelago. We hypothesised that: (1) topography, accessibility and spatial isolation drive the diversity and composition of plant communities in the CBNP and that (2) isolated areas contribute to high floristic regional diversity by supporting unique species assemblages. We expected high tree species diversity within the tropical limestone forests of the CBNP, but also that: (3) the abundance of non-tree species negatively affects tree regeneration diversity and abundance. Data were obtained from 90 random sample plots (500 m^2) and 450 sub-sample plots (25 m^2) in three areas of the CBNP. We differentiated four different plant species communities and found a total of 302 species belonging to 112 families. Tree species contributed 50% to total species richness. The distribution of different plant communities in the CBNP was driven mainly by topography; that is, the percentage of rock surface and slope and concomitant differences in soil depth. Contrary to our expectations, isolated areas did not contribute greatly to the CBNP's plant species diversity. It seems that isolated areas and, as in our case, rough topography, may act as natural barriers to seed dispersal, creating an environmental filter for tree species. Across the CBNP, there was no effect of non-tree species on tree species regeneration, but regeneration patterns differed between communities. In species-rich communities growing under favourable site conditions (e.g. low rock surface and slope), greater coverage by non-tree species had an increasingly negative effect on tree species richness and abundance in the regeneration layer. The opposite

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was observed in communities growing under harsh site conditions. We conclude that plant species diversity in the CBNP is high, particularly in easily accessible lowland areas where tree species contribute greatly to biodiversity. However, here, non-tree species can even restrict tree regeneration.

Keywords
Gamma diversity, heterogeneity-diversity relationship, plant species community, plant species diversity

Introduction

Plant species diversity and composition are important drivers of forest ecosystem functions and services. They provide habitat and resources for different taxonomic groups and food resources (e.g. fruits) for humans (Trejo and Dirzo 2002; Behera and Misra 2005; Seta et al. 2018). Plant species richness and species co-existence in forests are influenced by topography, soil characteristics and climate variables (temperature and precipitation parameters), as well as habitat heterogeneity and habitat size (Wright 2002; Bailey et al. 2010). In addition, natural and anthropogenic disturbances can contribute both to biodiversity gain and loss and to changes in species composition (Behera and Misra 2005; Mendes et al. 2016). Each forest type has unique characteristics in terms of both plant species diversity and its most important drivers. Thus, studies of distinct forest types and forest configurations can reveal new and unexplored patterns.

According to one fundamental ecological theory, environmental heterogeneity is crucial for the diversity, distribution and growth of plant species communities (Hutchinson 1957; Trichon 1997; Vivian-Smith 1997; Holl et al. 2013); differences in soil nutrients (Tateno and Takeda 2003; Yavitt et al. 2009) or micro-topographic variation (Trichon 1997; Vivian-Smith 1997; Tateno and Takeda 2003) lead to niche differentiation, inducing species co-existence. Plant species diversity also depends on habitat configuration, including geographic isolation or fragmentation (Quinn and Harrison 1988; Martin-Queller et al. 2017; Uhl et al. 2021). Isolated habitats can be characterised by distinct habitat conditions with a high diversity of specialised species (Quinn and Harrison 1988; Martin-Queller et al. 2017; Uhl et al. 2021). In contrast, Scheffer et al. (2006) found a negative effect of small habitat size and isolation on the biodiversity of shallow lakes and ponds in Britain due to limitations in habitat size, degree of connectivity and dispersal. In other studies, it was found that half of the native plant species richness was lost in small mixed dipterocarp forest fragments after a century of isolation (Turner et al. 1996). Therefore, the impact of isolation or fragmentation on plant species richness at local and regional scales must be explored in more detail for different forest types. This may be especially important for forest landscapes that are characterised by natural barriers, such as steep slopes and ridges or water bodies in island landscapes.

In addition to species diversity, interactions amongst vertical forest layers are important for forest development and functioning. The overstorey layer affects the understorey primarily via canopy cover (Berger and Puettmann 2000; Prieto et al. 2014) and litter quality (Zhang et al. 2010; Tsai et al. 2018). The overstorey layer provides

favourable habitats for, for example, ferns, lianas, epiphytes, herbs and epiphyllous organisms (Mezaka et al. 2020). The understorey contributes to the total species diversity of a forest ecosystem (Linares-Palomino et al. 2009) and affects soil properties, evaporation and humidity. Tree species regeneration as part of the understorey influences the composition and structure of the overstorey layer over the long term (Fang et al. 2014; Thrippleton et al. 2018; Pham et al. 2020). Understorey plant species assemblages may compete with tree regeneration for water, nutrients and light or may facilitate regeneration by, for example, protecting small trees from browsers (Nuttle et al. 2013). However, the relationship between overstorey and understorey depends on the forest type and on environmental conditions and may, therefore, vary with landscape heterogeneity (Laska 1997; Tardella et al. 2017) or with the impact of former (natural or anthropogenic) disturbance history.

Tropical and subtropical forests are known as remarkably diverse ecosystems and are considered biodiversity hotspots (Fangliang et al. 1997; Both et al. 2011). Their immense species richness makes complete sampling coverage difficult and underscores the importance of every study's contribution to the characterisation of the diversity of these forest ecosystems (Cicuzza et al. 2013). Plant species diversity and composition also play important roles in socio-economics, environmental protection and the living conditions of people who depend on forests and their products, especially in tropical forests of Southeast Asia (including Vietnam; Sodhi et al. 2009; Sun et al. 2009). In Vietnam, 11,373 plant species, belonging to 2,524 genera, 378 families and seven phyla have been identified; these include many species important for medical use (FSIV 2009). In 2006, the forested area was 12,874 million ha (38% forest cover) comprising of 10,410 million ha of natural forests and 2,464 million ha of plantations (FSIV 2009). In addition, the Vietnamese government has established 30 national parks and protected areas to protect and preserve precious genetic resources within natural forests (Pham and Nguyen 2018). To date, floristic research in Vietnam has concentrated on a few national parks, nature reserves and forest types. Here, we focused on the Vietnamese Cat Ba National Park (CBNP). This study aims to increase our knowledge of plant species diversity and the distribution of plant species in limestone forests of Vietnam, a forest type poorly studied up until now. The CBNP is located on a limestone archipelago and differs greatly from the mainland national parks of Vietnam in having many isolated islands and valleys and it is not known how this landscape configuration contributes to the plant species diversity and composition of the National Park or if the configuration affects the relationship between the overstorey and the understorey vegetation including tree regeneration. By surveying plant species in three different study sites of the CBNP representing in total ca. 4,000 ha, we hypothesised that; (1) topography, accessibility and spatial isolation are the main drivers of differentiation amongst plant communities in the CBNP. Further, we assumed that: (2) isolated areas contribute to high floristic regional diversity of the CBNP by supporting unique species assemblages. We also expected high diversity of tree species, but also that: (3) the abundance of non-tree species can negatively affect tree regeneration diversity and abundance. We assumed that this negative effect would be greater

in habitats characterised by adequate water and nutrient availability by inducing competition (Holmgren et al. 1997). A negative effect of the understorey on tree species regeneration could influence tree species diversity of the CBNP in the long term.

Our study aims to contribute to the knowledge of the autecology of different plant species and plant species assemblages within limestone forests of Vietnam as a potential basis for future monitoring and conservation programmes.

Methods

Study site

The CBNP is situated on Cat Ba Island, in the Tonkin Gulf, northern Vietnam. It lies ca. 45 km east of Haiphong City and 150 km south-east of Hanoi. Geographical coordinates are 20°44'N to 20°55'N (DM), 106°54'E to 107°10'E (DM) (Fig. 1) (Pham et al. 2020).

The CBNP is located on a limestone archipelago that consists of 366 islands and islets (CBNP 2005). The total CBNP area is 16,197 ha with ca. 10,932 ha of terrestrial island areas and 5,265 ha of marine areas (CBNP 2005, 2007). The average elevation is

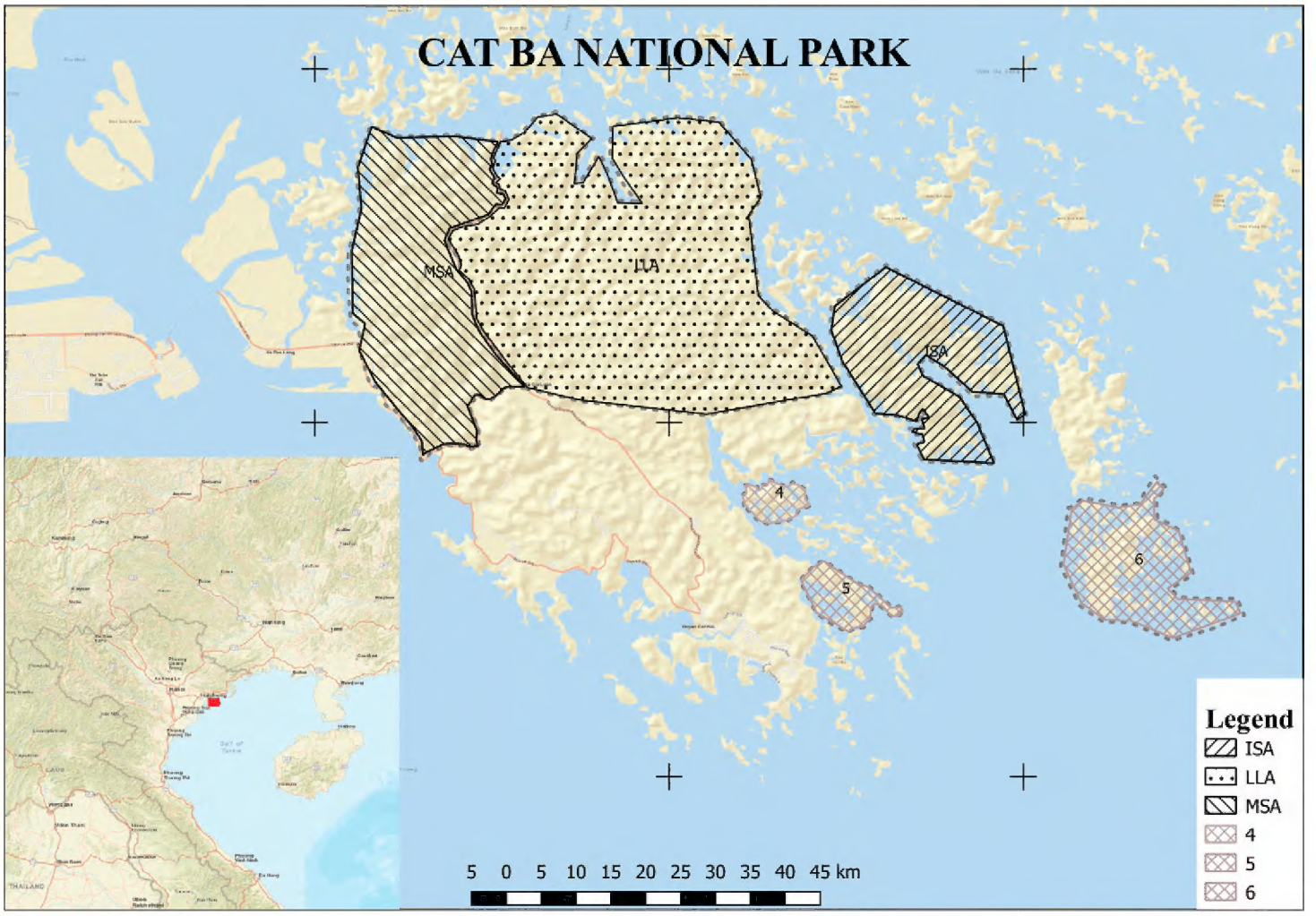

Figure 1. Location of Cat Ba National Park (CBNP), Haiphong, Vietnam. We collected data at three different study sites: MSA, a mid-slope area; LLA, a lowland area; ISA, an isolated area; 4, 5 and 6 are other restricted areas in the CBNP that were not considered for this study (Pham et al. 2020). Map data copyrighted by OpenStreetMap contributors and available from https://www.openstreetmap.org (CC BY-SA 2.0).

between 100 and 150 m a.s.l. with the highest peak of 331 m a.s.l. and average slopes ranging from 15° to 35° (CBNP 2007). The CBNP is characterised by two distinct seasons: the rainy season (from May to October) and the dry season (from November to April) with yearly rainfall from 1,500 to 2,000 mm. Average annual temperature is 23 °C and the average air humidity is approximately 86% (CBNP 2005; Le 2006).

Various ecosystems and forest types can be found in the CBNP and these include evergreen forests on limestone, wetland forest ecosystems in steep mountain valleys, mangrove forests, coral reefs and cave systems (CBNP 2005; Le 2006). The forest ecosystems include primary (undisturbed by direct human activity) evergreen broadleaf tropical rain forests, secondary evergreen broadleaf tropical forests in the lowlands (previously disturbed by human activity) and on limestone mountains, secondary moist evergreen restoration forests on limestone mountains and valleys, restored bamboo forests, wetland forests in the limestone valleys, mangrove forests and plantation forests (Carle and Holmgren 2003; CBNP 2007).

In 2004, Cat Ba Island was designated a UNESCO biosphere reserve because of its diverse flora and fauna (CBNP 2005). In total, 1,561 vascular plant species belonging to 842 genera and 186 families have been recorded across the different terrestrial ecosystems. Amongst them, 408 tree species have been observed in the CBNP in the past years by local authorities (CBNP 2007). Twenty-nine tree species listed in the IUCN Red List were recorded in the CBNP (Le 2006; CBNP 2007). Forty-three additional tree species are listed on the Vietnam Red List in terms of conservation (Le 2006; CBNP 2007). To allow the natural development of ecosystems and to protect precious plants and animals in the CBNP, six strictly protected zones were established, totalling 4,915 ha (Fig. 1). In these protected areas, management activities, such as timber logging, hunting or slash and burn, are prohibited. We chose three of the six restricted areas for our study that represent the three main conservation areas of the National Park. These three areas are characterised by primary and secondary evergreen broadleaf tropical forest ecosystems (Fig. 1). These areas also represent an accessibility gradient. The lowland area (LLA) (1,916.4 ha) is in the centre of the Park and is the most easily accessible of the three. The mid-slope area (MSA) (600 ha) lies in the north-western part of the Park and is characterised by steeper slopes compared to the LLA. The third area is an isolated area (ISA) (1,557.8 ha) and is located on a separate island in the eastern part of the Park. Its island situation isolates ISA from the two other study areas (Fig. 1). Note that in Fig. 1, some local villages were included into the boundaries of MSA, making the study area larger than the actual forested area.

Data sampling

We used the simple random sampling technique (Kleinn et al. 2009) to set up sample plots (Fig. 2). Thirty strips were created in each research area. In each strip, random sample plots were generated using random numbers to determine their coordinates. Two uniform random numbers U_{1i}, U_{2i} (the U interval from 0 to 1) were used each time to calculate $X_i = U_{1i} * X_{max}$, with $Y_i = U_{2i} * Y_{max}$ as coordinates for each random

sample plot, where X_{max} and Y_{max} were the largest coordinates of the area map (Fig. 2). If the coordinate (X_i, Y_i) appeared within the defined strip, this point was accepted as a sample plot point. Otherwise, the point was rejected and the procedure was repeated with two new U(s) random values (Fig. 2).

Based on this technique, a total of 90 random sample plots were created (30 plots in each of the three protected areas (LLA, MSA and ISA)). Each sample plot area was 500 m^2 in size (20 m × 25 m).

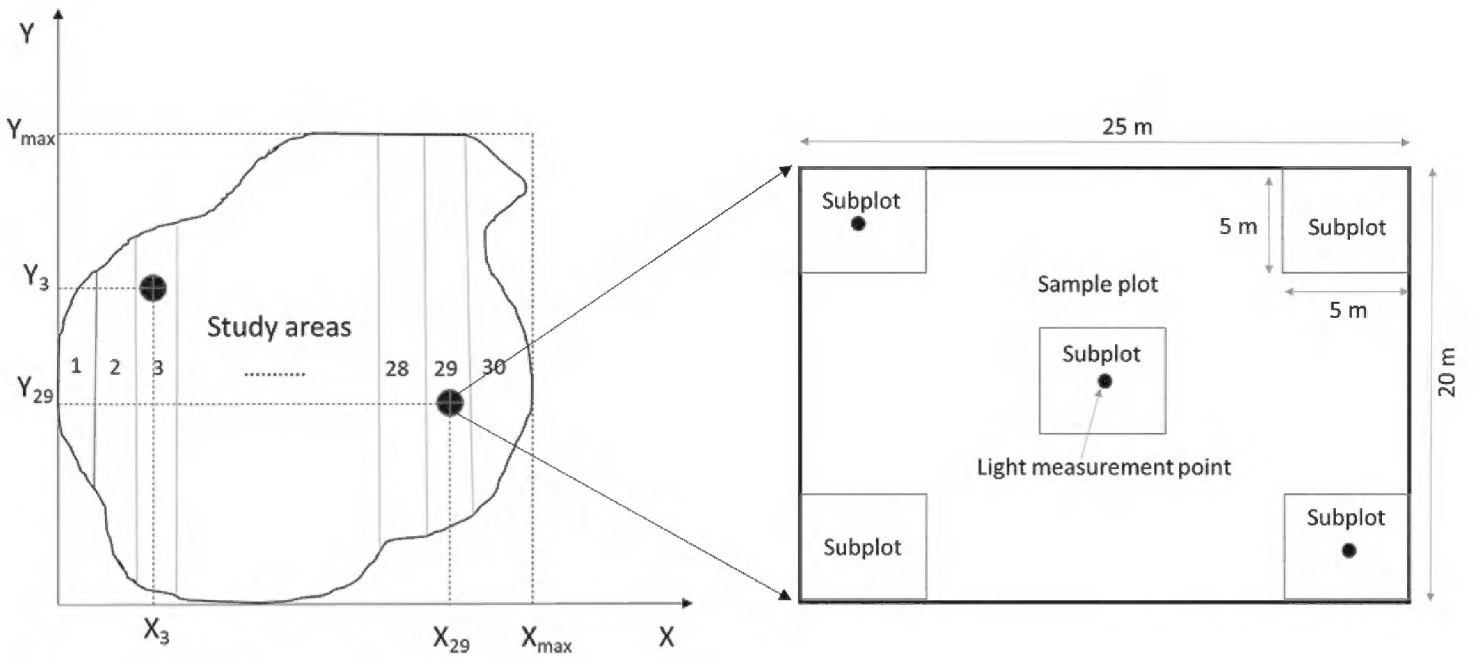

Figure 2. Sampling design scheme.

Overstorey tree layer

Within each sample plot, diameter at breast height (DBH) and height of all overstorey trees with DBH ≥ 5 cm were measured. We identified each individual tree to the species level. We defined species of the overstorey tree layer as tree species that now or in the future will be able to form the upper forest canopy. Botanists of the Northeast College of Agriculture and Forest (AFC) and from Cat Ba National Park assisted with identification. All recorded tree species were assigned to categories of threat according to the IUCN Red List categories (IUCN 2017).

Regeneration layer

We assigned individual trees, potentially able to reach the upper canopy in the future, with DBH < 5 cm to the regeneration layer. Regeneration was recorded on five subplots, which were established on five positions within each sample plot (Fig. 2) (Pham et al. 2020). Each subplot area was 25 m^2 (5 m × 5 m). Seedlings and saplings of all tree species were identified to the species level. Tree species found in the regeneration layer were also assigned to categories of threat following the approach for standing tree species.

Non-tree species layer

We additionally assigned plant species, other than trees and irrespective of their height, to the forest understorey and identified them to species level. We defined this layer as the non-tree species layer. Species included shrubs (even > 5 cm DBH), bamboo species, vines, medical plants and edible plants (MARD 2006; Sorrenti 2017). The non-tree species were recorded in the five subplots (Fig. 2) by estimating their coverage percentage. Coverage from all five subplots was then averaged to determine per plot coverage.

Growth site conditions

To characterise the growing conditions of plant species in the different plots and study areas, we recorded variables describing topography, soil conditions and light availability, as well as former impacts by humans.

As ***topographic variables*** (*T*), we recorded slope (T_SL), elevation (T_Ele) and percentage of rock surface area (T_RS) per sample plot. At the centre of each sample plot, the slope was measured with an inclinometer. Longitude, latitude and elevation were measured with a Garmin GPSMAP 64st device. A visually estimated mean value of rock exposure across the five subplots resulted in values for rock surface area (T_RS) per plot (%).

Soil conditions (*S*) included chemical and physical properties. Soil samples were collected at the centre of each sample plot using a soil auger (diameter 10 cm). A 20 cm core of the topsoil layer was sampled to analyse absolute soil moisture content (S_SM), soil humus content (S_SH), base saturation (S_BS), pH (S_pH), hydrolytic acidity (S_HA), total cation exchange capacity (S_CEC), soil texture (S_Sand, S_Silt, S_Clay) and percentage of rock in soil (S_RS). Soil depth (S_SD) was measured with a steel rod on the five subplots; the five values were then averaged. Samples were analysed in the soil laboratory of the Vietnam National University of Forestry. For details, see Pham et al. (2020) and Pham et al. (2022).

Light availability (*L*) was measured with a solariscope (SOL 300B, Ing.-Büro Behling, Wedemark) as an indirect site factor (L_ISF), which is the proportion of diffuse sunlight as a percentage of open field conditions. Measurements were conducted at 2 m above the ground on three diagonal subplots across the sample plot (Fig. 2).

After its establishment in 1986, the board of directors of the CBNP tried to reduce the human impact in the core zones of the CBNP by moving people outside the core zones. To date, however, many villages are still located close to the CBNP. Hence, activities of the local people, such as illegal logging and hunting, can still be detected. To roughly quantify a possible ***human impact*** (*H*), we counted footpaths (H_FP), tree stumps (H_STP) and poacher traps to catch animals (H_AT) on the plots as proxies for human activities.

Data analysis

To analyse plant species composition in the CBNP and to identify different forest communities, we used hierarchical cluster analysis with Ward's method using the function

'vegdist()' to create a Bray Curtis distance matrix, the function 'hclust()' to conduct a cluster analysis and the function 'cutree()' to draw a community dendrogram. These functions are implemented in the 'vegan' package in R (Oksanen et al. 2019).

To display the spatial distribution of communities in multidimensional space, we used the non-metric multidimensional scaling (NMDS) ordination method, based on abundance data. In the first step, we used the 'metaMDS()' function to run an NMDS and then used the 'envfit()' function to add environmental data into the NMDS graph using 'vegan' in R . We included all vegetation layers into the NMDS. Tree species of the overstorey and regeneration layers were combined to avoid duplication of species names.

To determine indicator species for identified forest communities, we used the function 'multipatt()' in the package 'indicspecies' (De Cáceres and Legendre 2009). The indicator species analysis calculates the specificity of a species as the number of occurrences of a species within a community relative to the number of occurrences across communities and the frequency of the species within a community as the relative number of occurrences per community. Multiplying specificity and frequency results in an indicator value between 0 (species not occurring in a specific forest community) and 1 (species occurring only and always in a specific community). The most significant indicator species identified amongst the tree and non-tree species were used to name the forest communities that were determined by cluster analysis.

To determine factors affecting community distribution in the CBNP, we correlated the NDMS axes' values with the environmental factors and human impact indicators. The function 'anova()' following a post-hoc Tukey-test with function 'glht()' in 'multcomp' package was used to compare these variables amongst communities.

We additionally applied different selection operators to build decision trees to weigh the predictors that characterised plant species communities (= the response). Forward selection of the predictors performed best. This method starts with an empty model and adds predictors to explain the response. Performance is estimated in each round using cross-validation. Only predictors with the highest performance increase are kept, then a new round is started. The maximum number of attributes to add was limited to seven to avoid overfitting; the iteration was aborted when performance no longer increased. This yielded a decision tree classifying the plant species communities. Classification trees represent a robust, non-parametric, binary procedure that partitions variance in the variation of communities through a series of splits in more homogeneous groups based on environmental factors or human impact variables (De'ath and Fabricius 2000; Cutler et al. 2007).

We contrasted plant species richness amongst the detected forest communities, species groups (tree and non-tree-species) and vegetation layers (overstorey tree, regeneration, non-tree layer) at different spatial scales. For alpha diversity, we compared plot-based species richness amongst communities using the 'anova()' function, followed by a post-hoc Tukey-test with function 'glht()' in the 'multcomp' package. To compare total species diversity in the identified communities, we used the 'iNEXT' package in R (Hsieh et al. 2016) to estimate the respective gamma diversity. The 'iNEXT' package applies different orders of Hill numbers (q) and quantifies diversity by applying rarefaction and extrapolation methods (Chao et al. 2014). We considered the

first three Hill numbers referring to species richness (q = 0), the true diversity of the Shannon Index, which is the exponential of the Shannon Index (q = 1) and Simpson diversity (q = 2) (Chao and Jost 2012; Hsieh et al. 2016). We estimated diversity for each defined forest community separately and across communities as an estimate for the gamma diversity of the CBNP.

To investigate how much each detected forest community contributed to the gamma diversity of the CBNP, we contrasted the estimated species pool of different combinations of communities to the species pool estimated for a combination of all detected communities. We also estimated the gamma diversity of tree and non-tree species of the CBNP and of different forest communities.

The relationship between non-tree species and the overstorey tree layer and between non-tree species and the regeneration layer was checked using linear regression models. We investigated the relationships across communities and for each community separately.

All statistical analyses were conducted using the statistical software R version 3.4.2 (R Core Team 2017). The level of significance for all statistical inferences was defined as p-value < 0.05.

Results

Forest communities of the CBNP

We identified four main communities that differ distinctly in species composition in Cat Ba National Park, (Fig. 3, Appendix 1). Each community has characteristic indicator species (Table 1). The most reliable indicators (highest indicator index value) amongst the tree and non-tree species provided the community names (Table 1, species characteristics are provided in Appendix 2). We defined the *Saraca dives* + *Calamus tetradactylus* community (SCt), the *Sterculia lanceolata* + *Chloris barbata* community (SCb), the *Ficus superba* + *Acanthus ebracteatus* community (FAe) and the

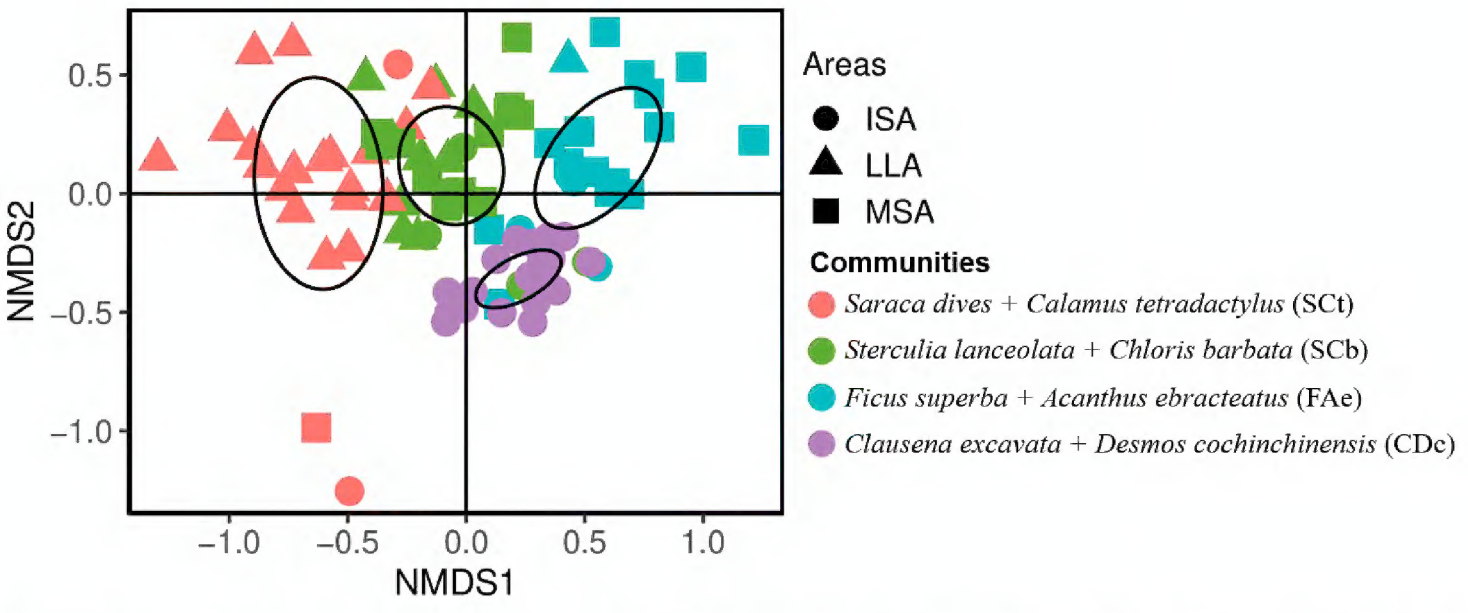

Figure 3. Spatial distribution of communities in NMDS analysis. The ellipses show the confidence levels at 95% of covariance of each community.

Clausena excavata + *Desmos cochinchinensis* community (CDc) (Appendix 2). Most indicator species (14 species) were associated with the SCt community, six species were associated with the SCb community and only four indicator species with the FAe community. For the CDc community, ten indicator species were identified (Table 1).

Ordination revealed that the SCt community was found mainly in the lowland area (LLA). The SCb community characterised a transition from the lowland to mid-slope area. The FAe community was associated with the mid-slope area and the CDc community with the isolated area (Fig. 3).

Table 1. Indicator species of the four identified forest communities. The eponymous tree and non-tree indicator species are given in bold. The growth form of each species is given as species group. See Appendix 8 for a list of all species detected within the study plots.

Species	Species group	Indicator value	p-value
***Saraca dives* + *Calamus tetradactylus* community (SCt)**			
Saraca dives	Tree	0.789	0.001
Calamus tetradactylus	Vine	0.681	0.001
Peltophorum pterocarpum	Tree	0.630	0.001
Ardisia gigantifolia	Shrub, medical plant	0.592	0.001
Garcinia oblongifolia	Tree	0.582	0.002
Gomphandra tonkinensis	Shrub, medical plant	0.496	0.002
Cinnamomum ovantum	Tree	0.469	0.011
Bauhinia coccinea	Shrub	0.445	0.008
Aglaia spectabilis	Tree	0.444	0.013
Ardisia silvestris	Shrub, medical plant	0.417	0.007
Mussaenda crosa	Shrub	0.401	0.014
Phoebe pallida	Tree	0.373	0.041
Caryota obtusa	Shrub	0.369	0.037
Phytele phantoideae	Shrub	0.369	0.034
***Sterculia lanceolata* + *Chloris barbata* community (SCb)**			
Sterculia lanceolata	Tree	0.694	0.001
Paramichelia baillonii	Tree	0.520	0.002
Zanthoxylum nitidum	Tree	0.500	0.001
Chloris barbata	Grass	0.423	0.003
Convolvulus parviflorus	Shrub	0.380	0.044
Markhamia cauda-felina	Tree	0.378	0.035
***Ficus superba* + *Acanthus ebracteatus* community (FAe)**			
Acanthus ebracteatus	Shrub	0.931	0.001
Ficus superba	Tree	0.418	0.009
Bursera tonkinensis	Tree	0.401	0.049
Connarus paniculatus	Vine	0.387	0.013
***Clausena excavata* + *Desmos cochinchinensis* community (CDc)**			
Clausena excavata	Tree	0.800	0.001
Microcos paniculata	Tree	0.775	0.001
Desmos cochinchinensis	Vine	0.644	0.001
Zephyranthes carinata	Herb	0.541	0.002
Helixanthera parasitica	Shrub	0.468	0.015
Pandanus tectorius	Shrub	0.448	0.008
Blumea lacineata	Herb	0.402	0.024
Syzygium jambos	Tree	0.400	0.032
Morinda citrifolia	Tree	0.387	0.017
Cnestis palala	Vine, medical plant	0.374	0.049

Forest structure and abiotic conditions of the forest communities

Forest structure differed amongst the four communities. On average, we found the lowest diameter at breast height (DBH), height (Ht), basal area (BA) and volume (Vol) in the FAe community, while the SCt community was characterised by the highest mean volume, DBH, basal area and height. The SCb community had the highest tree species richness, whereas the CDc community was the most species-poor in the overstorey layer (Table 2).

Community comparisons, as well as the decision tree analysis, showed that the communities FAe and CDc were associated with steeper slopes and a high percentage of rock surface area (Fig. 4, Table 3, Appendix 3). In contrast, the SCb and SCt communities were found in areas with deeper soils (Fig. 4, Table 3, Appendix 3). Although soils are shallower in the habitats of the FAe and CDc communities, their soil humus content (S_SH), soil moisture (S_SM) and cation exchange capacity (S_CEC) were high (Fig. 4, Table 3, Appendix 3) in the upper soil layers. Light conditions differed little between the four communities. Overall, SCb received the most light (Table 3, Appendix 3). Indicators of human impact were mainly associated with the communities SCt and SCb (Fig. 4).

Table 2. Forest structure of the different forest communities in the CBNP. The highest and lowest values are written in bold. Different letters indicate statistically significant differences amongst communities.

	SCt community	SCb community	FAe community	CDc community
DBH (cm)	**24.1 ± 4.47**^{c}	22.1 ± 5.22^{b}	**18.5 ± 4.83**^{a}	22.1 ± 3.68^{b}
Ht (m)	**12.58 ± 2.23**^{c}	10.68 ± 1.52^{b}	**9.32 ± 1.9**^{a}	10.52 ± 1.47^{b}
BA ($m^2.ha^{-1}$)	**36.4 ± 17.0**^{c}	29.1 ± 19.7^{b}	**21.1 ± 15.5**^{a}	27.8 ± 11.5^{b}
Vol ($m^3.ha^{-1}$)	**279.23 ± 160**^{c}	229.27 ± 193^{b}	**163.06 ± 157**^{a}	209.51 ± 108^{b}
Tree species richness	15.4 ± 6.1^{b}	**15.5 ± 6.0**^{b}	13.4 ± 2.8^{a}	**12.9 ± 2.6**^{a}

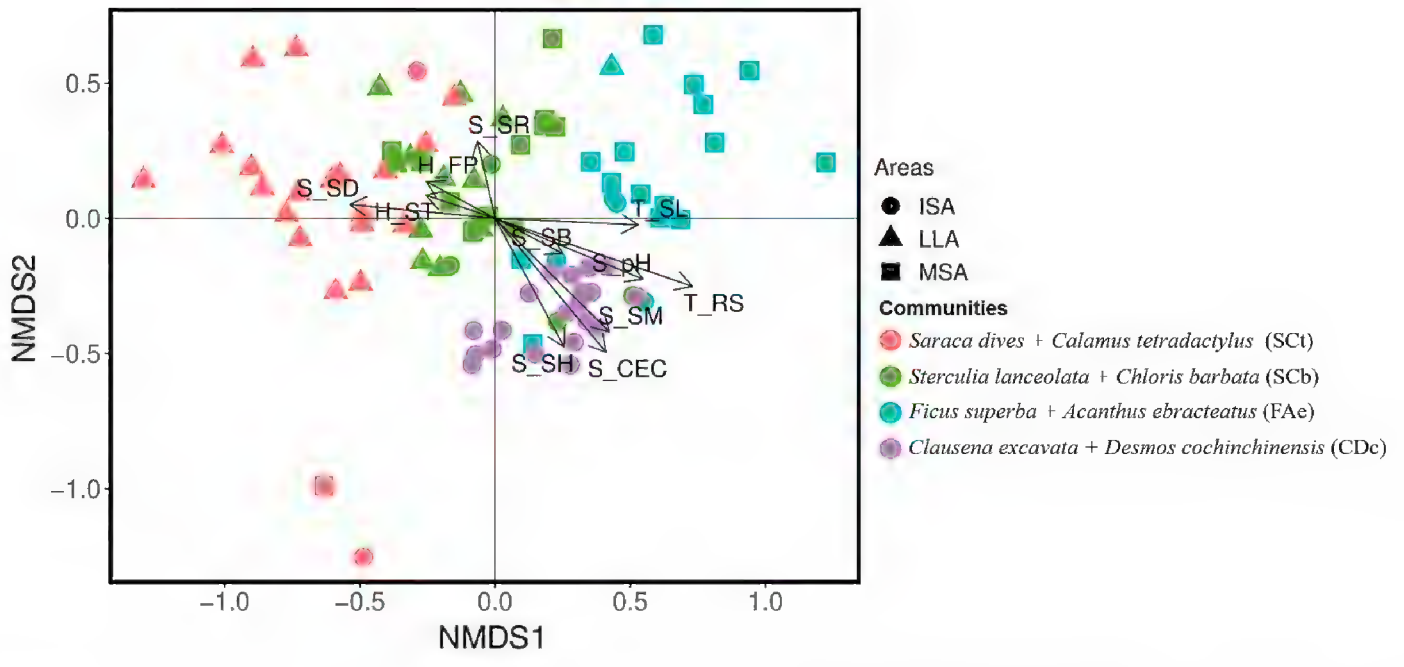

Figure 4. Correlation of environmental and human impact factors if significant (T = topographic variables, S = soil variables, H = human impact) with the NMDS axes. Length of the arrow indicates the strength of the correlation. Arrows in the same direction indicate a positive correlation of the variables with each other and a unidirectional response to NMDS axes. All variables that significantly correlated with the axes (p-value < 0.05) are shown. ISA = isolated area; LLA = lowland area; MSA = mid-slope area. The abbreviations for environmental and human disturbance factors are defined in Table 3.

Table 3. Mean values (± standard deviation) of environmental and human impact factors of the four communities. Superscript letters indicate statistically significant differences amongst the four communities. The highest and lowest values for each variable are written in bold.

Indicators	SCt community	SCb community	FAe community	CDc community
Number of sample plots	22	28	20	20
T_SL (Slope) (°)	**11.7 ± 8.77**^{a}	14.4 ± 9.44^{b}	**26.1 ± 10.82**^{d}	22.3 ± 8.42^{c}
T_RS (Rock surface) (%)	**20 ± 17.1**^{a}	35.6 ± 23.1^{b}	71.9 ± 19.3^{d}	**81.9 ± 12.6**^{c}
T_Ele (Elevation) (m)	74 ± 31.9^{b}	**62.7 ± 35.7**^{a}	87.2 ± 42.7^{c}	**89.1 ± 42.8**^{c}
S_SD (Soil depth) (cm)	**79.8 ± 39.0**^{c}	76.5 ± 34.0^{b}	**32.3 ± 17.9**^{a}	34.6 ± 23.9^{a}
S_SR (Rock in soil) (%)	**12.98 ± 23.05**^{c}	8.74 ± 14.85^{b}	8.53 ± 6.17^{b}	**5.83 ± 2.96**^{a}
S_SM (Soil moisture) (%)	**5.76 ± 5.5**^{a}	8.24 ± 5.2^{b}	**14.12 ± 3.9**^{d}	13.24 ± 3.3^{c}
S_Sand (Sand content) (%)	31.5 ± 10.9^{c}	29.8 ± 11.6^{b}	**25.2 ± 10**^{a}	**38.6 ± 16.6**^{d}
S_Clay (Clay content) (%)	**27.1 ± 11.19**^{a}	28.8 ± 7.88^{b}	**33.8 ± 5.99**^{b}	27.5 ± 9.21^{a}
S_SH (Soil humus content)	2.8 ± 1.47^{b}	**2.46 ± 1.02**^{a}	3.91 ± 1.58^{c}	**4.59 ± 1.02**^{d}
S_pH (pH value)	**4.77 ± 0.52**^{a}	5.10 ± 0.52^{b}	**5.58 ± 0.46**^{d}	5.47 ± 0.28^{c}
S_HA (Soil acidity)	5.20 ± 2.23^{b}	4.57 ± 1.72^{a}	**4.73 ± 1.74**^{a}	**5.39 ± 2.47**^{b}
S_BS (Base saturation) (%)	**55.5 ± 13.05**^{a}	59.9 ± 10.82^{b}	**63.7 ± 10.22**^{d}	61.9 ± 9.09^{c}
S_CEC (Cation exchange capacity)	**6.13 ± 1.47**^{a}	6.63 ± 1.30^{b}	8.07 ± 1.20^{c}	**8.28 ± 0.80**^{d}
H_FP (Footpaths) (N.plot^{-1})	**1.27 ± 0.45**^{c}	1.26 ± 0.49^{c}	1.07 ± 0.53^{b}	**1.00 ± 0.0**^{a}
H_Stp (Stumps) (N.plot^{-1})	**0.16 ± 0.37**^{b}	0.15 ± 0.36^{b}	**0.0 ± 0.0**^{a}	**0.0 ± 0.0**^{a}
H_AT (Animal traps) (N.plot^{-1})	0.62 ± 1.38^{b}	**1.01 ± 1.79**^{d}	0.78 ± 1.56^{c}	**0.43 ± 1.12**^{a}
L_ISF (Indirect site factor) (%)	8.80 ± 2.96^{b}	**9.56 ± 8.81**^{c}	**8.12 ± 2.15**^{a}	9.22 ± 3.30^{bc}

Differences in environmental factors among communities were also reflected in the differences in environmental factors among the study sites in which the communities were mainly located (see Figs 3, 4, Appendices 1, 4). For example, the average slopes in ISA and MSA were steeper than in LLA. As the FAe and CDc communities were associated mainly with the MSA and ISA sites, they were also characterised by higher slope values compared to the other two communities (Appendix 1). In addition, the ISA site had the highest percentage of rock surface as did the CDc community (Appendix 3).

Patterns of plant species diversity of the forest communities

Across communities, the non-tree species layer was, on average, more species-rich than the overstorey and regeneration layers, with the highest non-tree species richness found in the SCb community (Fig. 5). The overstorey tree layer was significantly more diverse in the SCt and SCb communities compared to the FAe and CDc communities (Fig. 5). A similar pattern was found for the regeneration layer (Fig. 5). Thus, the communities with the lowest plot-based species richness of the regeneration layer also had the lowest plot-based species richness in the overstorey tree layer.

Gamma diversity estimations identified significantly higher values for the communities SCt and SCb compared to the communities FAe and CDc. For the Hill number q = 2, the SCb community, which characterised the transition from the lowland to the

mid-slope area, was significantly more diverse than the other three communities; confidence intervals do not overlap. For all Hill numbers, the forest community associated mainly with the isolated area (CDc) had the lowest gamma diversity (Fig. 6). When plots of all four communities were combined, gamma diversity did not exceed the most diverse community, indicating that community assemblages are not complementary, but exhibit nested diversity.

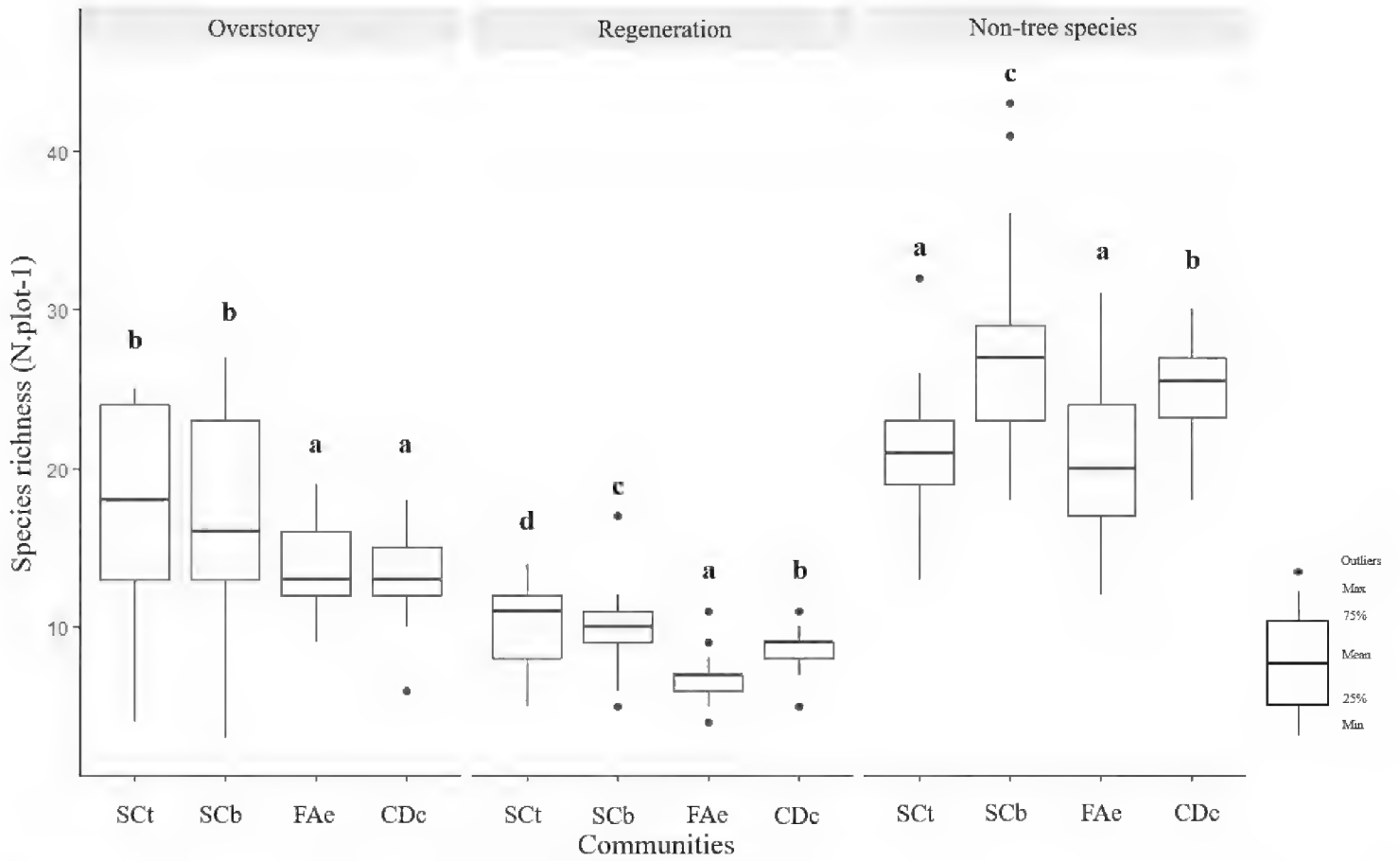

Figure 5. Boxplots of species richness of the three investigated layers in each forest community. Letters indicate statistically significant differences amongst communities. SCt; *Saraca dives* + *Calamus tetradactylus* community. SCb; *Sterculia lanceolata* + *Chloris barbata* community. FAe; *Ficus superba* + *Acanthus ebracteatus* community. CDc; *Clausena excavata* + *Desmos cochinchinensis* community.

When investigating the importance of each community to CBNP gamma diversity, we first estimated the species pools of different combinations of communities. We found that the SCb and SCt communities were most important for regional gamma diversity. When these communities were eliminated from community combinations, gamma diversity was greatly reduced as compared to the total species pool and to other community combinations (Appendix 5). If, however, the CDc and FAe communities were not included in the estimation procedure, the estimated species pool was not significantly different from the total species pool, indicating that these communities are mainly subsets of the species-richer communities (Appendix 5).

Gamma diversity patterns of the different communities were driven in large part by tree species (Fig. 7). Tree species were significantly less diverse in the communities FAe and CDc compared to the other two communities (Fig. 7, Appendix 6). For the

non-tree species, the difference between the two community groups (SCb, SCt vs. FAe, CDc) was not as pronounced for q = 0 (Fig. 7). For q = 1, the SCb community was significantly more diverse than the communities FAe and CDc. For q = 2, SCb was more diverse than all other identified communities (Fig. 7, Appendix 6).

Tree and non-tree species contributed nearly equally to the diversity of the CBNP (Table 4). However, in the SCt and SCb communities, tree species diversity was higher than non-tree species diversity, while in the other two communities, the converse was true (Table 4).

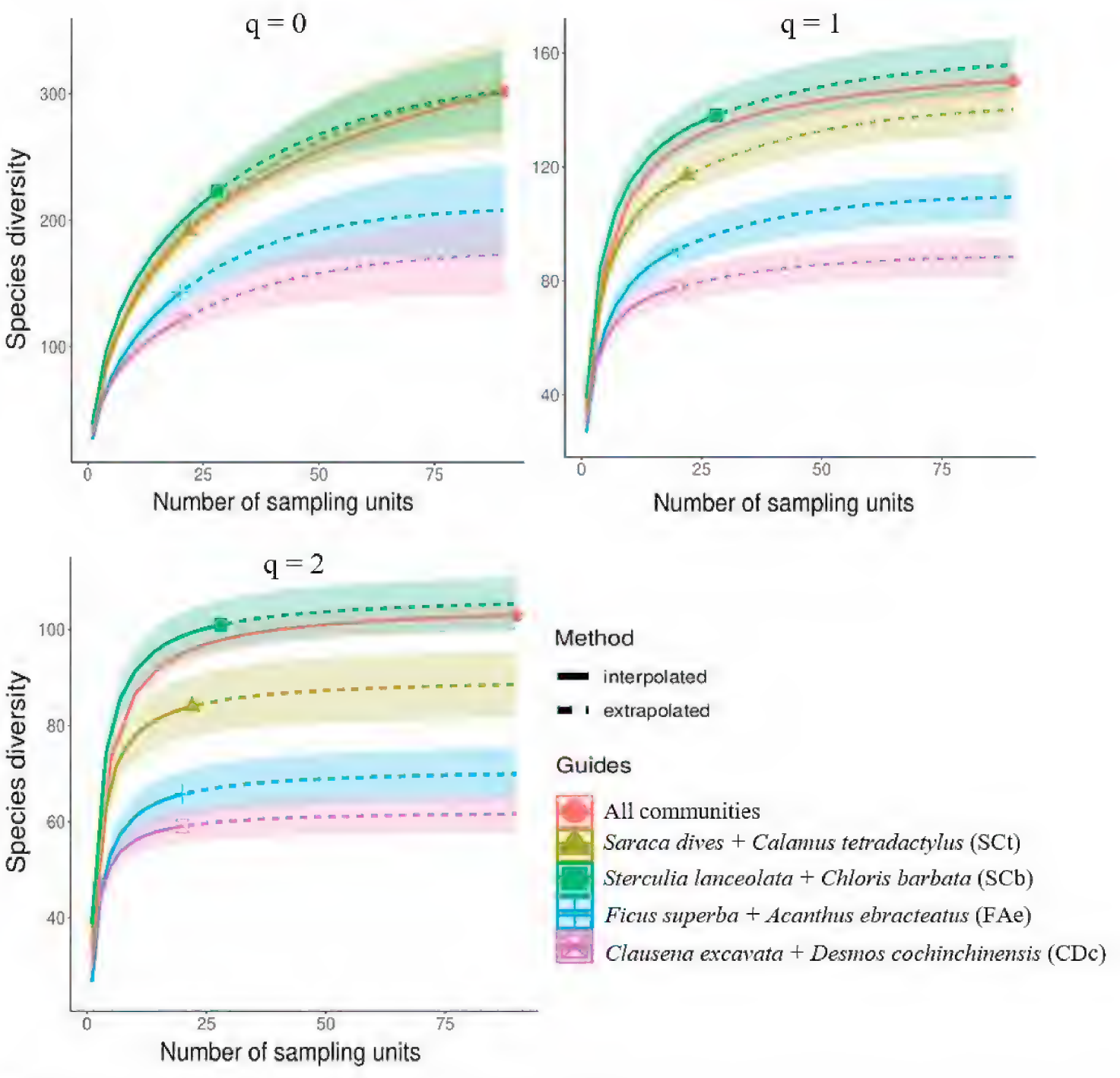

Figure 6. Estimated gamma diversity for different Hill numbers and forest communities. q = 0: species richness; q = 1: Shannon diversity; q = 2: Simpson diversity. The red colour represents the estimated gamma diversity when all communities are considered for estimation. Yellow-green: *Saraca dives* + *Calamus tetradactylus* community (SCt). Green: *Sterculia lanceolata* + *Chloris barbata* community (SCb). Light-blue: *Ficus superba* + *Acanthus ebracteatus* community (FAe). Pink: *Clausena excavata* + *Desmos cochinchinensis* community (CDc). Graphs were extrapolated to a sample size of 90 plots.

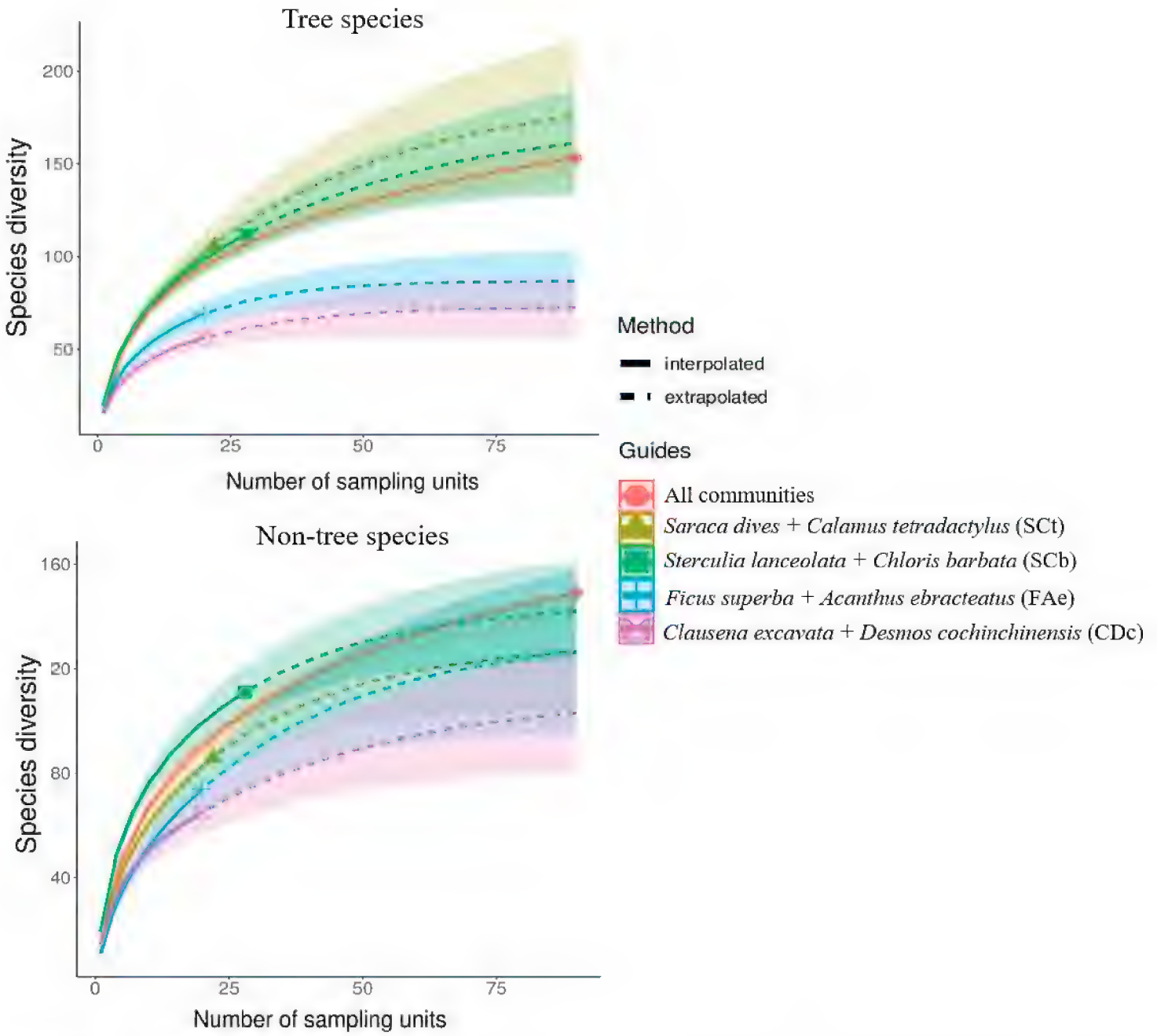

Figure 7. Gamma diversity patterns of tree species and non-tree species of the different communities. The graphs show species richness (Hill number q = 0, including 95% confidence interval). Red: all four communities, Yellow-green: *Saraca dives* + *Calamus tetradactylus* community (SCt), Green: *Sterculia lanceolata* + *Chloris barbata* community (SCb), Light-blue: *Ficus superba* + *Acanthus ebracteatus* community (FAe), Pink: *Clausena excavata* + *Desmos cochinchinensis* community (CDc). For Hill numbers q = 1 and q = 2, see Appendix 6. Graphs were extrapolated to a sample size of 90 plots.

Table 4. Estimated species pool by species group and community for q = 0. The value in brackets indicates the 95% confidence interval.

Layer	All communities	SCt community	SCb community	FAe community	CDc community
All species	367.7 (339.3 ÷ 417.7)	316.7 (261.6 ÷ 415.5)	317.0 (275.5 ÷ 391.5)	211.4 (178.2 ÷ 275.8)	178 (146.4 ÷ 249.3)
Tree species	190.8 (170.4 ÷ 235.0)	190.5 (144.7 ÷ 290.7)	175.7 (140.7–253.4)	87 (75.6–118.1)	73.2 (61.4 ÷ 110.7)
Non-tree species	177.6 (161.9 ÷ 212.4)	130.2 (105.0 ÷ 189.0)	145.7 (126.2–190.5)	133.1 (98.9 ÷ 214.6)	110.6 (80.5 ÷ 199.4)

Relationships between vertical forest layers

We did not find a significant relationship between species richness of the non-tree layer and that of the tree regeneration layer. We also found no effect of species richness of the overstorey tree layer on species richness of the non-tree species layer or the regeneration layer (Fig. 8).

Across all communities, there was also no significant effect of the coverage of the non-tree species layer on the species richness or abundance of the regeneration layer (Fig. 9a, c). However, at the community level, we found that coverage of the non-tree species layer negatively affected both abundance and richness of the regeneration layer in the SCb community and of richness in the SCt community. In contrast, coverage by the non-tree species layer positively influenced the richness of the regeneration layer in the FAe community (Fig. 9b, d).

We did not observe any significant effect of species richness or coverage of the non-tree species layer on tree abundance or richness of threatened tree species in the regeneration layer (Appendix 7).

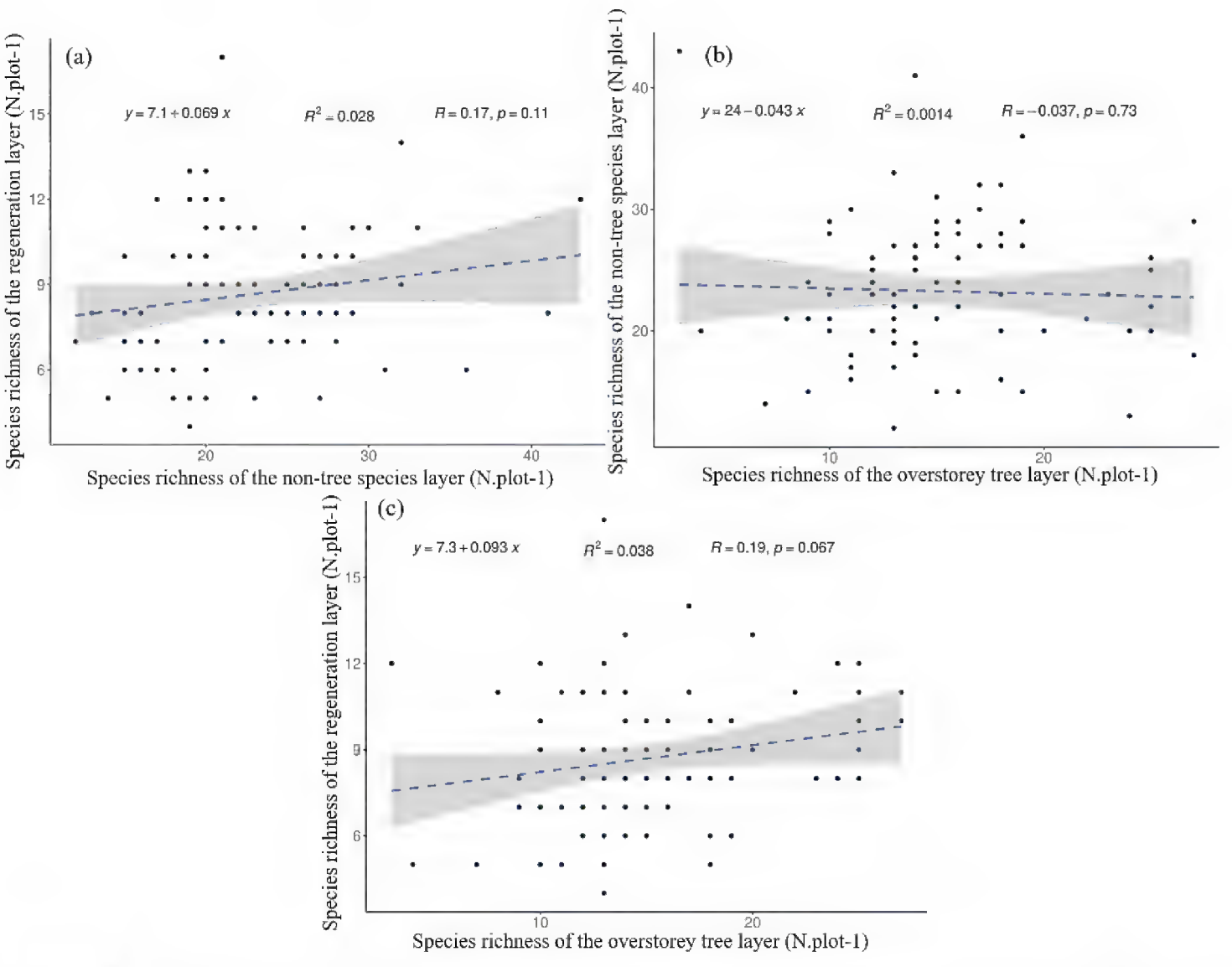
(a)
y = 7.1 + 0.069 x
R² = 0.028
R = 0.17, p = 0.11
Species richness of the regeneration layer (N.plot-1)
Species richness of the non-tree species layer (N.plot-1)
(b)
y = 24 − 0.043 x
R² = 0.0014
R = −0.037, p = 0.73
Species richness of the non-tree species layer (N.plot-1)
Species richness of the overstorey tree layer (N.plot-1)
(c)
y = 7.3 + 0.093 x
R² = 0.038
R = 0.19, p = 0.067
Species richness of the regeneration layer (N.plot-1)
Species richness of the overstorey tree layer (N.plot-1)

Figure 8. Linear regression models of plot-based species richness relating: **a** species richness of the non-tree species layer and species richness of the regeneration layer **b** species richness of the overstorey tree layer and species richness of the non-tree species layer and **c** species richness of the overstorey tree layer and species richness of the regeneration layer. The shaded area indicates the 95% confidence interval.

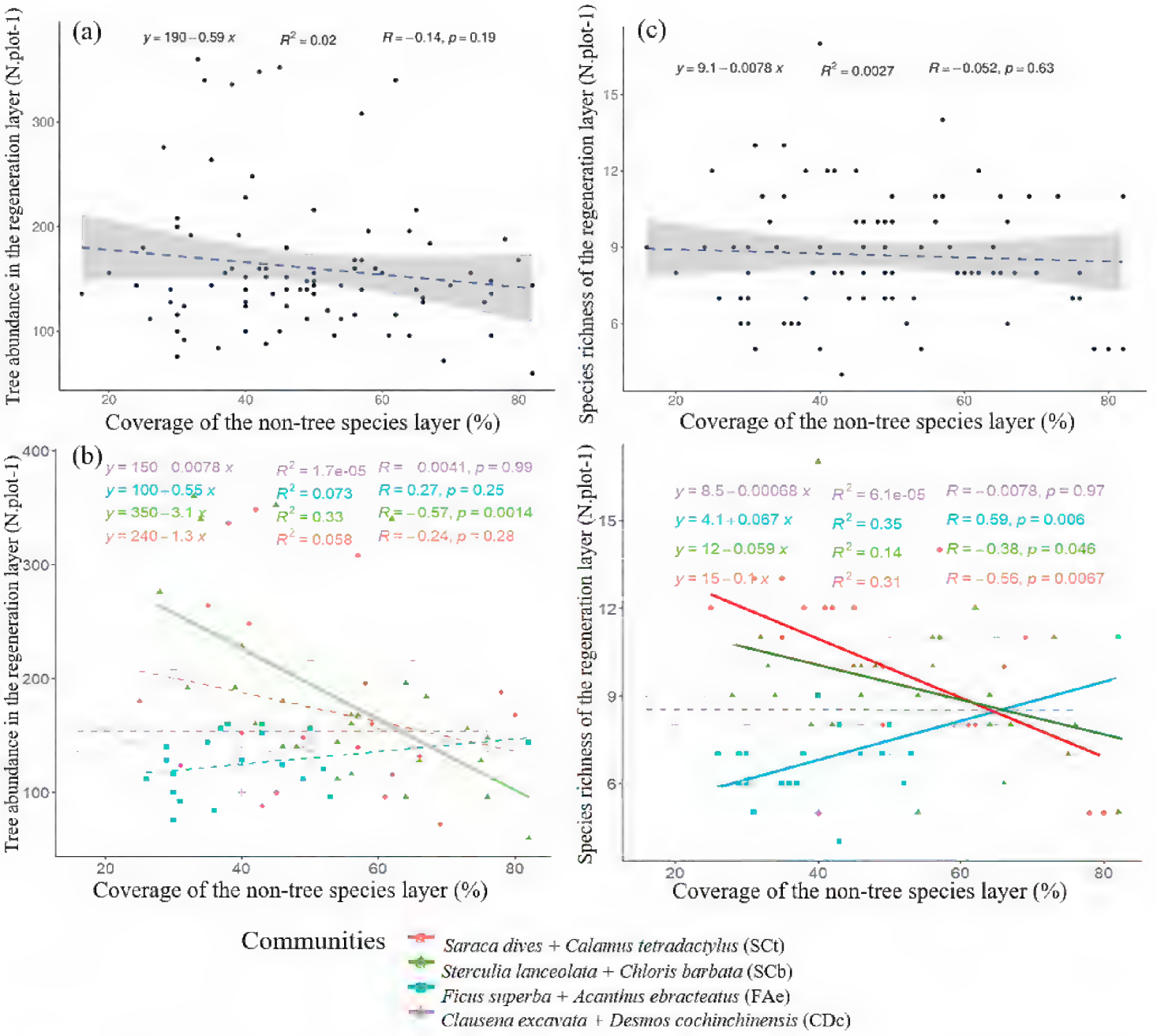
(a)
y = 190 − 0.59 x
R² = 0.02
R = −0.14, p = 0.19
Tree abundance in the regeneration layer (N.plot-1)
Coverage of the non-tree species layer (%)
(c)
y = 9.1 − 0.0078 x
R² = 0.0027
R = −0.052, p = 0.63
Species richness of the regeneration layer (N.plot-1)
Coverage of the non-tree species layer (%)
(b)
y = 150 − 0.0078 x
R² = 1.7e-05
R = −0.0041, p = 0.99
y = 100 − 0.55 x
R² = 0.073
R = 0.27, p = 0.25
y = 350 − 3.1 x
R² = 0.33
R = −0.57, p = 0.0014
y = 240 − 1.3 x
R² = 0.058
R = −0.24, p = 0.28
Tree abundance in the regeneration layer (N.plot-1)
Coverage of the non-tree species layer (%)
y = 8.5 − 0.00068 x
R² = 6.1e-05
R = −0.0078, p = 0.97
y = 4.1 + 0.067 x
R² = 0.35
R = 0.59, p = 0.006
y = 12 − 0.059 x
R² = 0.14
R = −0.38, p = 0.046
y = 15 − 0.1 x
R² = 0.31
R = −0.56, p = 0.0067
Species richness of the regeneration layer (N.plot-1)
Coverage of the non-tree species layer (%)
Communities
Saraca dives + Calamus tetradactylus (SCt)
Sterculia lanceolata + Chloris barbata (SCb)
Ficus superba + Acanthus ebracteatus (FAe)
Clausena excavata + Desmos cochinchinensis (CDc)

Figure 9. Linear regression models of the coverage of non-tree species and species richness and abundance of the tree regeneration layer. Graphs (**a**) and (**c**) show the relationship between the coverage of non-tree species with the abundance and species richness of tree regeneration across all communities, graphs (**b**) and (**d**) for the four communities. Dashed lines show statistically non-significant, solid lines show significant correlations. To improve visibility, we did not include the confidence intervals for (**b**) and (**d**).

Discussion

Topographic heterogeneity drives the spatial distribution of forest communities in the CBNP

We distinguished four forest communities in the CBNP that differ in forest structure and are characterised by different environmental conditions (Fig. 3, Tables 1, 2, Appendix 1). Topographic variables, in combination with soil conditions, turned out to be important factors influencing the differences in plant species composition across the CBNP. Topographic heterogeneity can result in different microclimatic conditions, affecting temperature and soil moisture at small scales, thus influencing the abundance and distribution of plant species (Vivian-Smith 1997; Seta et al. 2018). In addition,

topographic heterogeneity indirectly acts on plant species composition and diversity through drainage and by differences in the hydraulic regime, which results in different growing conditions for plants on ridges, slopes and in valleys (Trichon 1997). These characteristics may also affect seed erosion and seed accumulation, leading to differences in plant species distributions (Vivian-Smith 1997; Holl et al. 2013).

We found that the SCt and SCb communities occurred mainly on sites characterised by deep soils, whereas the FAe and CDc communities were found on sites with rough terrain (steep slopes and high rock surface), but with relatively high soil nutrient content (high soil humus content and CEC) (Fig. 4, Table 3, Appendices 1, 4). Our environmental characterisation of the communities corresponded well to the investigated study sites. The SCt and SCb communities characterised the lowland area in transition to the mid-slope study area, while the CDc community was associated mainly with the isolated area, characterised by steep slopes. Our results are in line with Zhang et al. (2021), who identified topography as the main factor determining niche differentiation of tree species in heterogeneous tropical limestone forests of China. Topography influenced soil depth and, thereby, most likely determined water availability and drought stress, factors that may have shaped species distribution.

Topographic heterogeneity can also influence light availability, an important determinant of plant species distribution (Zhu et al. 2016). It also affects forest composition by influencing regeneration patterns (Tateno and Takeda 2003). However, in our case, the indirect site factor (L_ISF), which we used as a proxy for light availability, did not affect plant species distributions (Fig. 4, Table 3, Appendix 4). It is important to mention that the gradient of light availability recorded across our study sites was quite low, indicating a relatively homogeneous canopy cover across the CBNP.

Although indicators of human impact could not be clearly connected to plant species distribution, observed differences in the forest communities of the different study areas could have reflected human influence, which was strongest in the lowland area. In the lowland area, with the communities SCt and SCb, species richness was highest (Figs 4, 5, Table 3). In contrast, other studies found negative effects of human disturbance on species diversity; humans extract certain tree species with subsequent effects on species composition (Blanc et al. 2000; Do et al. 2017). Chazdon (2003), however, concluded that forest recovery could be rapid even after large-scale human disturbances when soil and aboveground vegetation were not heavily impacted. In addition, Dao and Hölscher (2018) found a positive correlation between the occurrence of footpaths and the density of tree species used for non-timber forest products. This suggests a positive effect of human activity on some early-successional species. Other studies have confirmed the strong potential of tropical forests to recover after historical disturbances (Lusk and Smith 1998; Bayliss-Smith et al. 2003), but also underscore the role of historical disturbances, whether anthropogenic or natural, in shaping species composition.

We identified several indicator species for the four forest communities that provided valuable information on species-environment relationships. While species of the communities SCt and SCb seemed to be restricted to deep soils, indicator species in the FAe and CDc were able to tolerate harsh soil conditions, such as a high percentage of rock surface and shallow mineral soils (Guo et al. 2017). They were also able to overcome

potential dispersal filters due to the island isolation of the ISA. The bird-dispersed *Clausena excavata*, for example, is characterised by rapid germination, thereby avoiding the risk of desiccation in shallow soils. High seedling survival under various environmental conditions makes this species both a successful invader outside its native range and a successful coloniser (Vieira et al. 2010). Supporting results by Santo-Silva et al. (2021) demonstrated that isolation favours the abundance of disturbance-adapted pioneer tree species. The annual herb *Blumea lacineata*, another indicator in the CDc community, is also characterised by an effective dispersal strategy and is classified as a weed species (Wester 1992). On the other hand, *Sterculia lanceolata*, an indicator species of SCb, can be characterised as a mid- to late-successional species on deeper soils (Zhang et al. 2013). Its co-existence with the tropical weed species *Chloris barbata* (Holm et al. 1979) in the CBNP suggests that this community and its assemblage of indicator species characterise a successional stage after disturbance in lowland and mid-slope areas. Lower DBH and tree heights in this community, as compared to the SCt community of the lowlands, support this assumption. The species assemblage of the *Saraca dives* + *Calamus tetradactylus* reliably characterises lowland sites, as *Saraca dives* is a dominant species in foothills and in valleys with high and constant water availability in limestone forests (Zhang et al. 2021).

Thus, our study underscores the value of using identified indicator species or groups of species for an overall assessment of the environmental conditions in tropical limestone forests of Southeast Asia. By monitoring certain indicator species, shifts in environmental conditions can be reliably detected.

Differences in forest community composition do not drive the biodiversity of the CBNP

We identified in total 302 species belonging to 112 families in the CBNP (Table 4, Appendices 5, 8) within the 90 recorded sample plots. The total species pool was estimated at 368 species. We found that, as compared to other studies, plant species diversity in the CBNP was quite high. For example, diversity was higher than that of transitional rainforest vegetation in southwestern Ethiopia (from 130 to 139 species) (Assefa et al. 2013), neotropical primary and secondary forests (100 species found on two 1 ha plots (van Andel 2001), or subtropical forests in China (240 species in 27 plots of up to 900 m^2 (Both et al. 2011). It was less diverse, however, than rainforests in Columbia (442 vascular plant species in 0.9 ha; (Galeano et al. 1998) or seasonal dry tropical forests in Mexico (917 species in 20 representative sites of 0.1 ha; (Trejo and Dirzo 2002). Numbers are comparable with forests of Dinagat Island in the Philippines where 432 native plant species have been recorded (Lillo et al. 2019). In Malaysian tropical rain forests, 825 species in 50 ha forest inventory plots have been detected (Fangliang et al. 1997). Although differences in species numbers among the aforementioned studies may also be due to different experimental designs and scales of inventory (Ferraz et al. 2004; Cicuzza et al. 2013; Júnior et al. 2014), our results indicate that plant species diversity in the CBNP is comparable to other tropical and subtropical forests worldwide. Interestingly, non-tree species contributed roughly 50% to total species diversity (Table 4) emphasizing both the importance of different growth forms for biodiversity and con-

firming other studies (Gentry and Dodson 1987; Linares-Palomino et al. 2009). The forest communities FAe and CDc, characterizing rough and rocky terrain, had a higher share of non-tree species than those of the lowland and mid-slope areas, indicating that this species group is shaped by stochastic assembly processes, while the distribution of tree species is mainly driven by environmental differences among habitats (Both et al. 2011). Similarly, isolation seems to have acted as a stronger barrier for tree than for non-tree species (Hill and Curran 2003; Martin-Queller et al. 2017).

In contrast to our expectations, the heterogeneity we found in forest community composition did not appear to drive overall plant species diversity of the CBNP. The linkage between isolation and species diversity has been investigated in previous studies (Quinn and Harrison 1988; van Andel 2001; Slik et al. 2003; Scheffer et al. 2006; Chytrý et al. 2010). Isolated conditions can promote species diversity and the distinctiveness of communities (Ferraz et al. 2004), and can also drive speciation, leading to species endemism (EI-Bana 2009; Chytrý et al. 2010). Our findings indicate that the isolated area has the lowest species diversity in our study (Figs 6, 7, Appendix 5). This supports the conclusion by van Andel (2001) that relative isolation can also have a negative effect on species diversity. Slik et al. (2003) confirmed that diversity was negatively correlated with isolation and habitat size in North-eastern Borneo forests. Our results, therefore, suggest that rough terrain conditions in combination with the isolated location function as a strong dispersal and establishment filter that only a subset of the plant species can overcome. Such species are characterized by good dispersal ability (see above). The missing complementarity in species diversity among communities, however, indicates that the species assemblages colonizing the isolated area are instead a subset of richer species communities. Species colonizing the isolated sites can therefore be characterized as generalists growing under various site conditions (Vieira et al. 2010; Santo-Silva et al. 2021).

Our results also confirm the theory that larger areas boost high species diversity. The two species-rich SCt and SCb communities (Figs 3, 6, Table 4, Appendix 5) were located mostly on the main island of the CBNP; this presumably provided more habitats and better habitat connectivity with positive effects on the dispersal ability of species (MacArthur and Wilson 1967; Hill and Curran 2003; Martin-Queller et al. 2017). This agrees with Scheffer et al. (2006), who stated that local diversity is reduced in response to isolation through dispersal limitation. They also implied that larger local habitat patches and greater connectivity facilitate regional biodiversity. Turner et al. (1996) even found that a long period of isolation in lowland tropical forests in Singapore was a major contributor to species loss.

The species-rich SCb and SCt communities were associated with greater soil depth, while the percentage of rock surface and slope were correlated with species-poorer communities (FAe and CDc communities) (Fig. 4, Table 3). Slope and rock outcrops have a huge effect on soil cover in our research areas (Chytrý et al. 2010; Seta et al. 2018), influencing soil nutrients (Chytrý et al. 2010) and water availability (Zhang et al. 2021). This seems not only to result in differences in community composition as discussed before, but also in different numbers of tree and non-tree species. Tree species diversity was more strongly influenced than non-tree species by differences in topography, with more tree species colonizing the lowlands. The Simpson diversity of non-tree species was par-

ticularly high in the SCb community. Here the presence of indicator *Chloris barbata* suggested an impact of former disturbance. We do not have, however, enough information on former anthropogenic or natural disturbance events to make a definitive connection.

Humans can have a huge influence on floristic diversity; there are numerous examples from around the world. For example, Júnior et al. (2014) found that human activities changed tree species diversity and forest structure in semi-deciduous forests in Brazil. Assefa et al. (2013) found that anthropogenic interferences reduced species diversity in southwest Ethiopian forests. In our case, indicators of human impact and species-rich forest communities were positively associated (Fig. 5, Table 2). These results may indicate that the natural recovery potential of a species after historical disturbances is high (van Andel 2001; EI-Bana 2009). In any case, reconstruction of former disturbances would be useful to evaluate the potential for tree species recovery as well as to understand the effects of former disturbances on current species composition. However, as differences in human impact and environmental conditions among communities and study sites interact, we cannot verify a potential impact of former human disturbance on plant species diversity and composition in the CBNP.

Relationship between vertical forest layers

Across communities, we found no interactions amongst forest layers (Both et al. 2011), but found contrasting patterns for the different communities. In the two species-rich communities (SCb and SCt) found on deep soils, we detected negative effects of non-tree species coverage on tree species richness and abundance in the regeneration layer (Figs 8, 9b). It is well known that tree regeneration competes with herbaceous species on sites with sufficient water and nutrient availability (Both et al. 2011). Interestingly, under harsh environmental conditions in the CDc communities and also in the FAe (Fig. 9d), coverage by non-tree species appeared to have neutral (CDc) to positive (FAe) effects on the tree regeneration species richness; this supports the hypothesis that changes in water availability, such as those induced by more shallow soils, can shift plant interactions from competition to facilitation (Bertness and Callaway 1994; Holmgren et al. 1997). Along the steep slopes with high rock coverage, non-tree species can improve conditions for tree regeneration, for example, by trapping litter and humus. This, in turn, can improve water and nutrient status, supporting seedling germination and survival (Yirdaw et al. 2015; Yirdaw et al. 2019). This may also explain higher soil moisture values found in the topsoils of the FAe and CDc communities as compared to SCt and SCb. In addition, litter and humus accumulation may generally improve seed storage, preventing rapid erosion.

Competition between tree regeneration and non-tree species in the SCt and SCb communities may also have resulted from former canopy disturbances. Increased light levels induce understorey growth with potential negative effects on tree regeneration. The light-demanding weed species *Chloris barbata*, identified as an indicator species in the SCb community, may be an indication of former disturbances as are the higher values of human impact indicators in SCt and SCb. However, the light availability measured for this study was around 9.17% ± 6.4% (mean ± sd) and homogeneous across communities.

Limitations of the study

Although we have considered many environmental factors and indicators of human impact to explain plant species composition and diversity in the CBNP, we acknowledge some shortcomings. We did not explicitly consider climatic factors (Slik et al. 2003; Cicuzza et al. 2013), such as rainfall and temperature. However, since sites were close to one another (compare Fig. 1), we did not expect great differences in climatic conditions. We also do not have detailed information on the disturbance history of the CBNP, even though evolutionary or historical disturbance processes may control the distribution of certain species in certain sites (Trejo and Dirzo 2002; Tuomisto et al. 2003; Chytrý et al. 2010). Finally, factors such as geographical distance or tectonics may also have played a role in the observed patterns of plant species composition and diversity; both of these factors might affect environmental conditions, habitat formation and floral assemblages (van Andel 2001; Slik et al. 2003; Júnior et al. 2014). In future research, it may also be worth focusing on plant functional groups, which would require more research into the autecology of the different tree and non-tree species.

Conclusions

Our study demonstrates that plant species composition and diversity in the CBNP vary strongly at the regional scale. Contrary to our expectations, the isolated island site did not contribute much to total plant species richness. Species found there seemed well adapted to the harsh conditions, but were also found at other sites and can, therefore, be classified as generalists.

We also showed that environmental factors are important drivers of plant species composition and species diversity in the CBNP with non-tree species contributing about 50% to total species richness. Our data indicate that this species group is less prone than tree species to environmental filtering. Furthermore, the coverage of non-tree species negatively impacted species richness of tree regeneration on sites with sufficient water and nutrient availability (*Sterculia lanceolata* + *Chloris barbata* and *Saraca dives* + *Calamus tetradactylus* community). Under harsh environmental conditions, non-tree species appeared to facilitate tree regeneration richness of the *Ficus superba* + *Acanthus ebracteatus* community, underscoring the important function of non-tree species to forest development in these tropical forests on limestone. The *Sterculia lanceolata* + *Chloris barbata* and the *Saraca dives* + *Calamus tetradactylus* community, found mainly in lowlands in transition to mid-slope conditions, contribute most to plant species diversity in the CBNP.

From these findings, we conclude that plant species composition and diversity in the CBNP is rich, with tree and non-tree species contributing equally to this diversity, but with higher tree species diversity in the lowlands. For future conservation management, the protection of tree species, for example, from illegal logging activities, should be one priority for managers of the CBNP. This is particularly important as the area most accessible to the local population is characterised by tree species-rich forest communities. In

general, the main island contributes most to plant species richness in the CNBP due to the availability of microsites and connectivity amongst habitats. Thus, monitoring of species diversity and composition and conservation management to prevent fragmentation should focus on these areas. Here and beyond the CBNP, the dynamics of the identified indicator species groups will help to detect future changes in environmental conditions.

The identified forest communities with their indicator species assemblages provide fundamental information on the interactions between plant species distribution and environmental conditions in limestone forests of Vietnam and may also help to characterise the limestone forests beyond the borders of the CBNP.

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Appendix 1

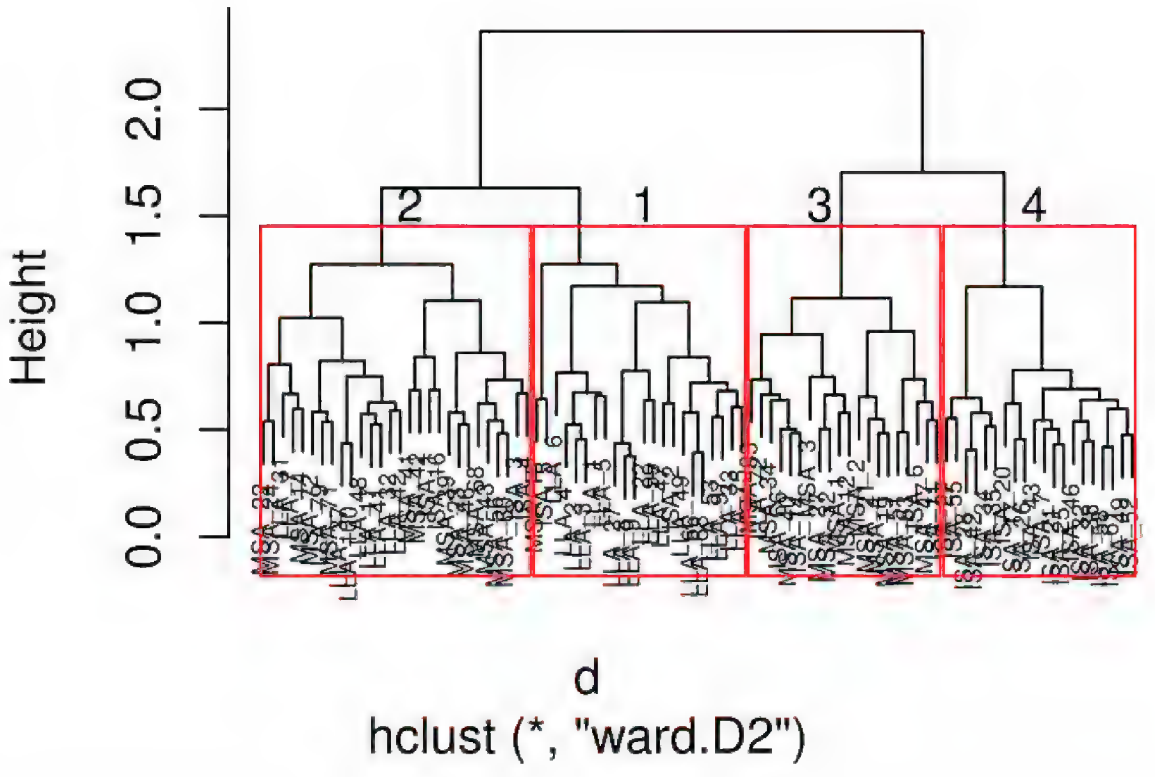
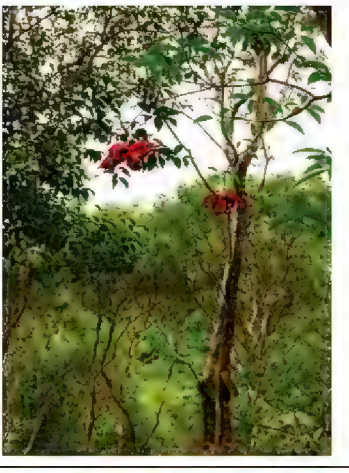
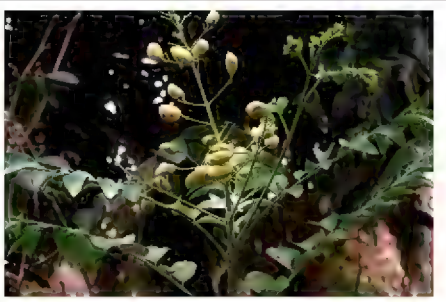


Figure A1. Communities' dendrogram in Cat Ba National Park. The numbers 1, 2, 3 and 4 showed the order of forestry communities after hierarchical cluster analysis. **1,** *Saraca dives* + *Calamus tetradactylus* community (SCt); **2,** *Sterculia lanceolata* + *Chloris barbata* community (SCb); **3,** *Ficus superba* + *Acanthus ebracteatus* community (FAae); **4,** *Clausena excavata* + *Desmos cochinchinensis* community (CDc). The "Height" axis shows the clustering height value associated with the Ward clustering method. The text of each branch showed the acronym of sample plots. LLA, low land area; MSA, mid-slope area; ISA, isolated area.

Appendix 2

Table A1. The information of representative species of the four communities. If not stated otherwise, photographs were taken by Van Vien Pham.

Species information	Image
Species: *Saraca dives* Family: Fabaceae Character: Small timber, tree height around 7–8 m. This species distributes near the stream, canals, water sources or humid areas, thick forests; distributed from north to central Vietnam.	
Species: *Calamus tetradactylus* Family: Arecaceae Character: Vines, It grows in evergreen forest and scrub between 1 and 1000 m elevation and in Delta areas. This species has valuable in craft making and trade in Vietnam.	
Species: *Sterculia lanceolata* Family: Sterculiaceae Character: Small timber tree, this species grows in mountainous areas, especially the hillsides in the midlands. The tree has large green leaves all year round and is suitable for moist areas. Flowers look like a star shape and in red. Distributed from Nnorth to central Vietnam.	
Species: *Chloris barbata* Family: Poaceae Character: Annual grass; distribution in dry places, especially coastal areas.	
Species: *Ficus superba* Family: Moraceae Character: This species is a small to medium timber tree species, tree height is from 5–15 m. It grows favourably in rich nutrient soil, with good moisture and drainage, is also a drought-tolerant species, not fussy about cultivated soil. This species has a very strong regeneration. Its distribution is throughout Vietnam.	 Source: https://giahuygarden.vn

Species information	Image
Species: *Acanthus ebracteatus* Family: Acanthaceae Character: Shrub trees with a height from 1–3 m. This species has a wide distribution; can be found in many habitats, such as in dense and open forests, coastal, valleys and swampy areas, water banks, estuarine areas and moist forests.	
Species: *Clausena excavata* Family: Rutaceae Character: Small timber tree. Tree height is around 5–6 m. It distributes from north to Ccentral Vietnam.	 Source: http://www.biotik.org/laos/species/c/claex/claex_03_en.html
Species: *Desmos cochinchinensis* Family: Annonaceae Character: Climber, branches whitish or rusty-red hairy, petals hairy, fruits red. It grows in stunted, poor forests.	 Source: https://www.ydhvn.com/public/news/cay-duoc-lieu-cay-gie-nam-bo-chap-chai-hoa-de-long-den-desmos-cochinchinensis-lour

Appendix 3

Table A2. The environmental and human activity characteristics in the three study sites (LLA, MSA and ISA) in Cat Ba National Park. The values represent the mean and standard deviation of 30 plots per study site (in total 90 plots). Small letters indicate significant differences at $p \leq 0.05$ between the three areas. The "multicomp" package was used to calculate differences between the three study sites (Hothorn et al. 2008). The acronym column shows the abbreviation of the factor. T, terrain factors; S, soil properties; L, light availabilities; and H, human disturbances.

Factors	Acronym	Average	LLA	MSA	ISA
Slope (°)	T_Sl	17.23 ± 10.71	13.70 ± 9.67^a	19.02 ± 10.38^b	21.85 ± 10.62^c
Rock surface (%)	T_RS	44.49 ± 31.62	22.71 ± 23.02^a	56.71 ± 22.84^b	71.99 ± 23.07^c
Elevation (m)	T_Ele	75.33 ± 38.92	78.06 ± 37.02^b	66.57 ± 37.40^a	78.35 ± 42.30^b
Soil depth (cm)	S_SD	61.78 ± 38.77	75.89 ± 40.24^b	51.97 ± 31.25^a	45.67 ± 32.84^a
Rock in soil (%)	S_SR	9.59 ± 15.95	11.31 ± 19.83^b	10.75 ± 14.96^b	5.50 ± 3.77^a
Soil moisture (%)	S_SM	8.98 ± 5.72	5.98 ± 5.26^a	11.06 ± 4.40^b	12.41 ± 4.72^c
Sand (%)	S_Sand	31.45 ± 12.86	32.40 ± 11.26^b	24.75 ± 7.35^a	35.76 ± 16.55^c
Silt (%)	S_Silt	40.10 ± 8.18	41.95 ± 7.35^b	41.73 ± 5.48^b	35.37 ± 9.62^a
Clay (%)	S_Clay	28.45 ± 9.48	25.64 ± 10.47^a	33.52 ± 5.25^c	28.86 ± 8.61^b
Soil humus content (%)	S_SH	3.11 ± 1.49	2.67 ± 1.32^a	2.76 ± 1.24^a	4.20 ± 1.44^b
pH	S_pH	5.10 ± 0.56	4.79 ± 0.50^a	5.40 ± 0.53^b	5.39 ± 0.36^b
Hydrolytic acidity (mmol /100 g)	S_HA	5.01 ± 2.11	5.12 ± 1.98^b	4.58 ± 1.97^a	5.20 ± 2.38^b
Cation exchange capacity (mmol / 100 g)	S_CEC	6.92 ± 1.53	6.12 ± 1.43^a	7.33 ± 1.11^b	7.96 ± 1.22^c
Base saturation (%)	S_BS	58.88 ± 11.66	55.34 ± 12.09^a	62.78 ± 11.11^b	61.64 ± 9.31^b
Indirect site factor	L_ISF	9.17 ± 6.40	8.21 ± 2.75^a	10.37 ± 11.68^b	9.81 ± 3.39^b
Footpaths	H_FP	1.19 ± 0.45	1.25 ± 0.43^b	1.17 ± 0.57^a	1.11 ± 0.31^a
Stumps	H_STP	0.11 ± 0.31	0.21 ± 0.41^b	0.02 ± 0.15^a	0.00 ± 0.00^a
Animal traps	H_AT	0.65 ± 1.42	0.54 ± 1.16^a	0.33 ± 2.03^b	1.22 ± 0.95^a

Appendix 4

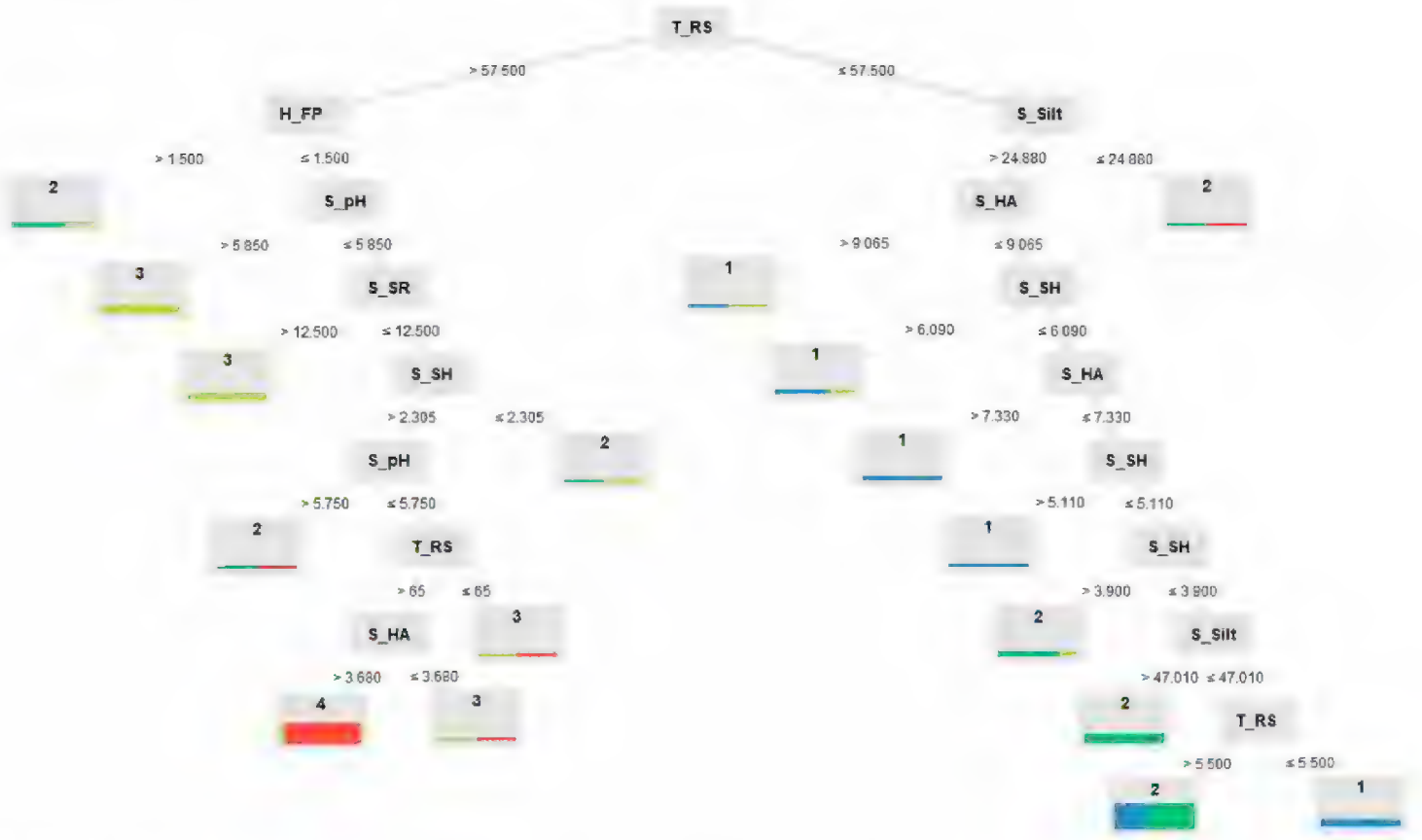


Figure A2. Classification tree of abiotic factors differentiating amongst communities. The regression tree shows independent environmental factors most closely related to the variation of communities. The communities were shown at the bottom of each branch of the independent environmental factors. The graph classifies environmental factors according to predictive strength (top to bottom). Abbreviations of the abiotic factors are defined in Table 3 and Appendix 3. The numbers give the communities: **1** = *Saraca dives* + *Calamus tetradactylus* community. **2** = *Sterculia lanceolata* + *Chloris barbata* community. **3** = *Ficus superba* + *Acanthus ebracteatus* community. **4** = *Clausena excavata* + *Desmos cochinchinensis* community.

Appendix 5

Table A3. Estimated species pool of the CBNP. The estimation was based on all communities and for different combinations of communities. The value in the brackets represents the lower and upper confidence interval at 95%. SCt; *Saraca dives* + *Calamus tetradactylus* community. SCb; *Sterculia lanceolata* + *Chloris barbata* community. FAe; *Ficus superba* + *Acanthus ebracteatus* community. CDc; *Clausena excavata* + *Desmos cochinchinensis* community. The highest and lowest estimated values for the different community combinations are written in bold.

	Species richness (q = 0)	**Shannon diversity (q = 1)**	**Simpson diversity (q = 2)**
Estimated species pool for all communities (SCt+SCb+FAe+CDc)	367.7 (339.3 ÷ 417.7)	159.8 (154.4 ÷ 165.2)	105.4 (102.9 ÷ 108.9)
Combination of communities:			
SCb+FAe+CDc	358.4 (318.1 ÷ 429.6)	149 (142.6 ÷ 155.5)	97 (94.2 ÷ 100.8)
SCt+FAe+CDc	334.7 (300.8 ÷ 394.4)	147.9 (141 ÷ 154.8)	97.5 (94.2 ÷ 102.1)
SCt+SCb+CDc	354.7 (324.4 ÷ 408.5)	160.1 (154.1 ÷ 166)	106.4 (103.4 ÷ 110.8)
SCt+SCb+FAe	**377.9 (343.1 ÷ 437.9)**	**166.6 (160.6 ÷ 172.6)**	**109.7 (106.3 ÷ 114.3)**
FAe+CDc	**244.3 (209.3 ÷ 313.2)**	**106.8 (100.8 ÷ 112.8)**	**71.4 (68.8 ÷ 75.3)**
SCb+CDc	338.6 (296.9 ÷ 413.9)	151.1 (143.7 ÷ 158.5)	99.9 (96.2 ÷ 104.5)
SCb+FAe	357.1 (313.6 ÷ 433.2)	160.7 (153.4 ÷ 168.1)	104.7 (100.3 ÷ 109.6)
SCt+CDc	328 (283.9 ÷ 407.5)	147.9 (139.68 ÷ 156.2)	97.7 (93.2 ÷ 102.7)
SCt+FAe	327.5 (289.4 ÷ 394.3)	158 (149.3 ÷ 166.7)	104.6 (99.16 ÷ 110)
SCt+SCb	356.4 (319.6 ÷ 420.2)	161.5 (154.3 ÷ 168.7)	106.8 (103 ÷ 111.6)

Appendix 6

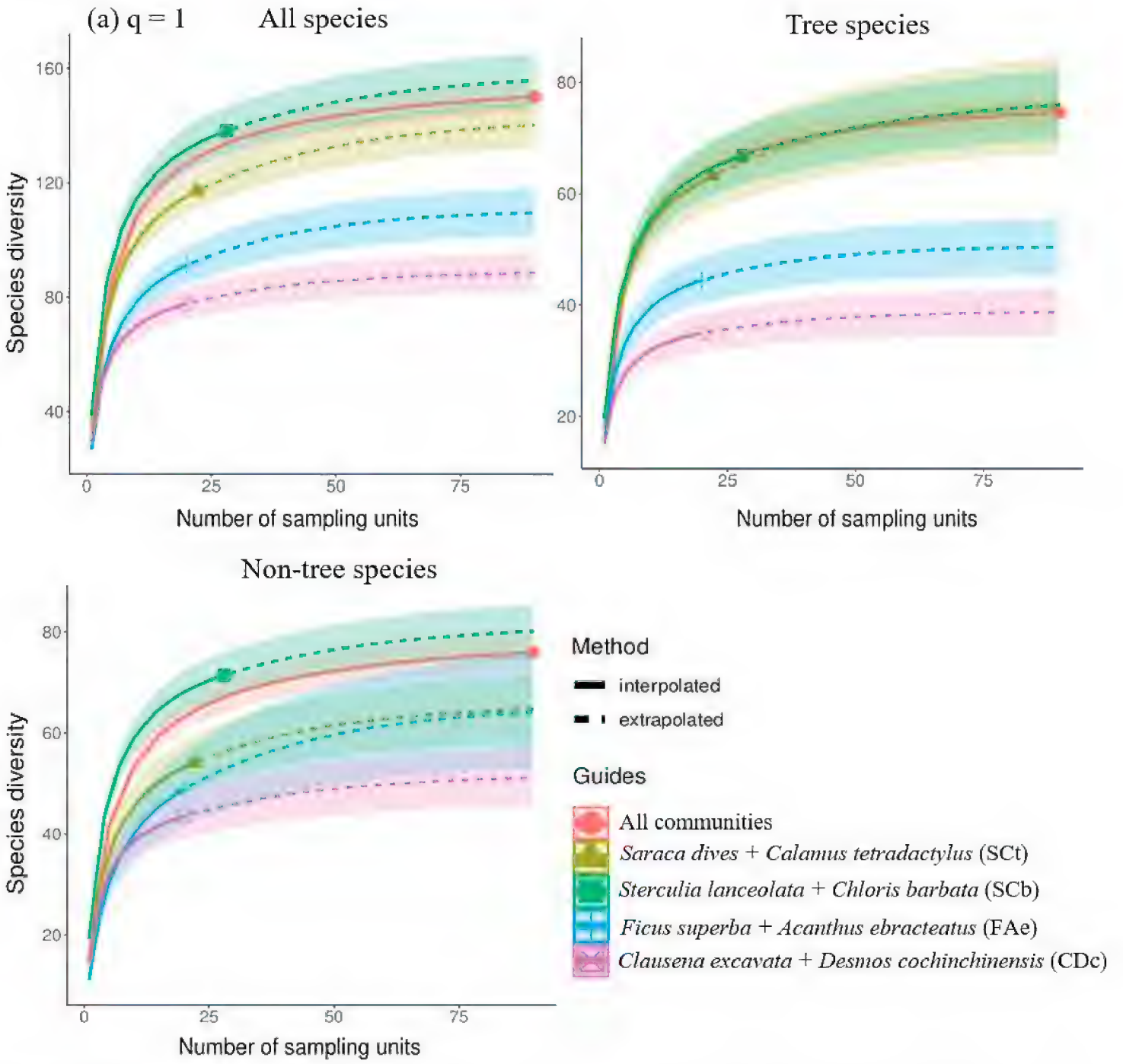


Figure A3. Species diversity patterns of the tree and non-tree species. The graphs show the Shannon (q = 1) and Simpson diversity (q = 2) (Hill number) from iNEXT analysis. The red colour represented the total tree species of all four communities (gamma diversity). Yellow-green colour represented the *Saraca dives* + *Calamus tetradactylus* community (SCt). The green colour represented the *Sterculia lanceolata* + *Chloris barbata* community (SCb). Light-blue represented *Ficus superba* + *Acanthus ebracteatus* community (FAe) and pink colour represented *Clausena excavata* + *Desmos cochinchinensis* community (CDc). The fade of the line showed the confidence level at 95%.

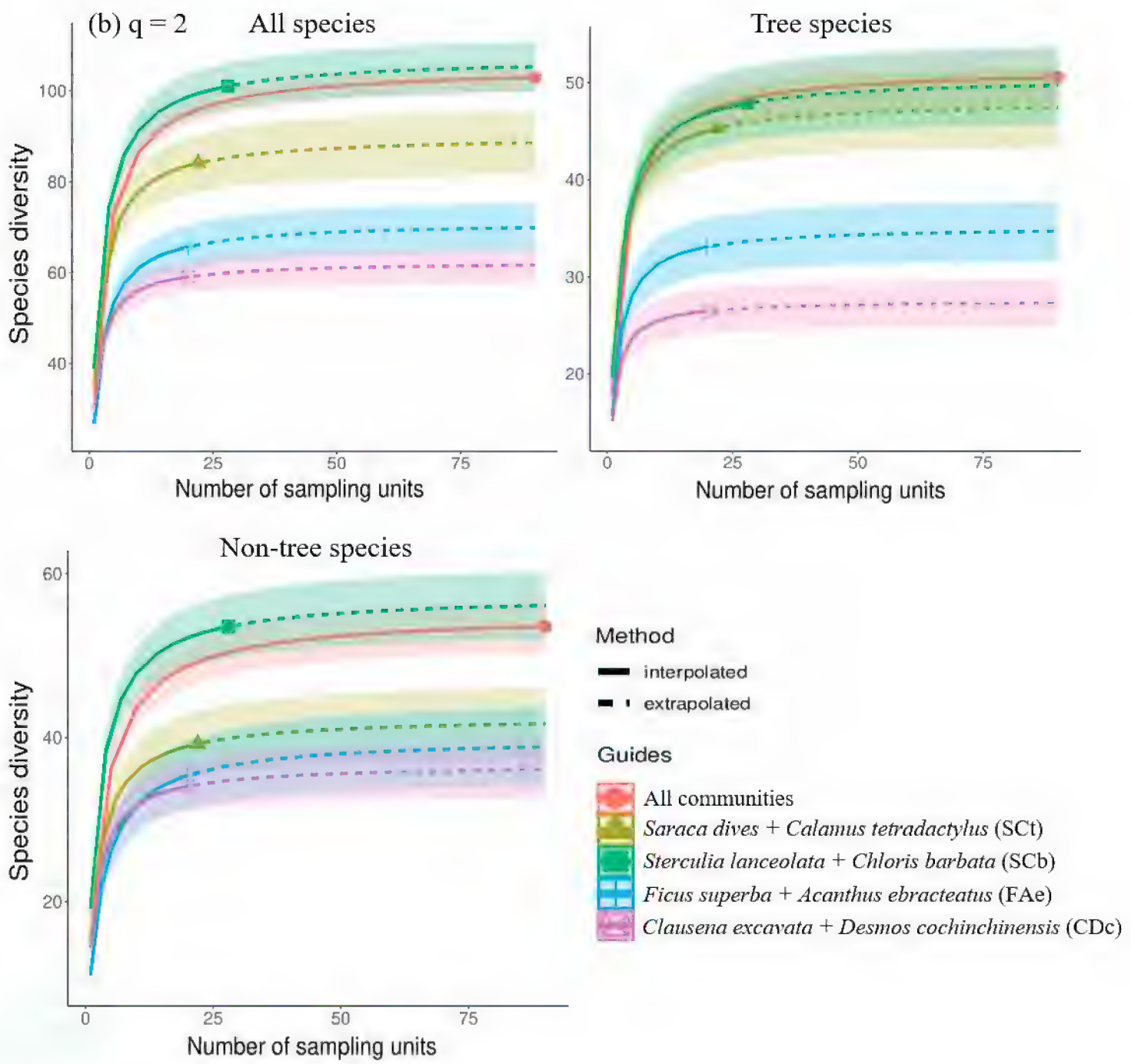


Figure A3. Continued.

Appendix 7

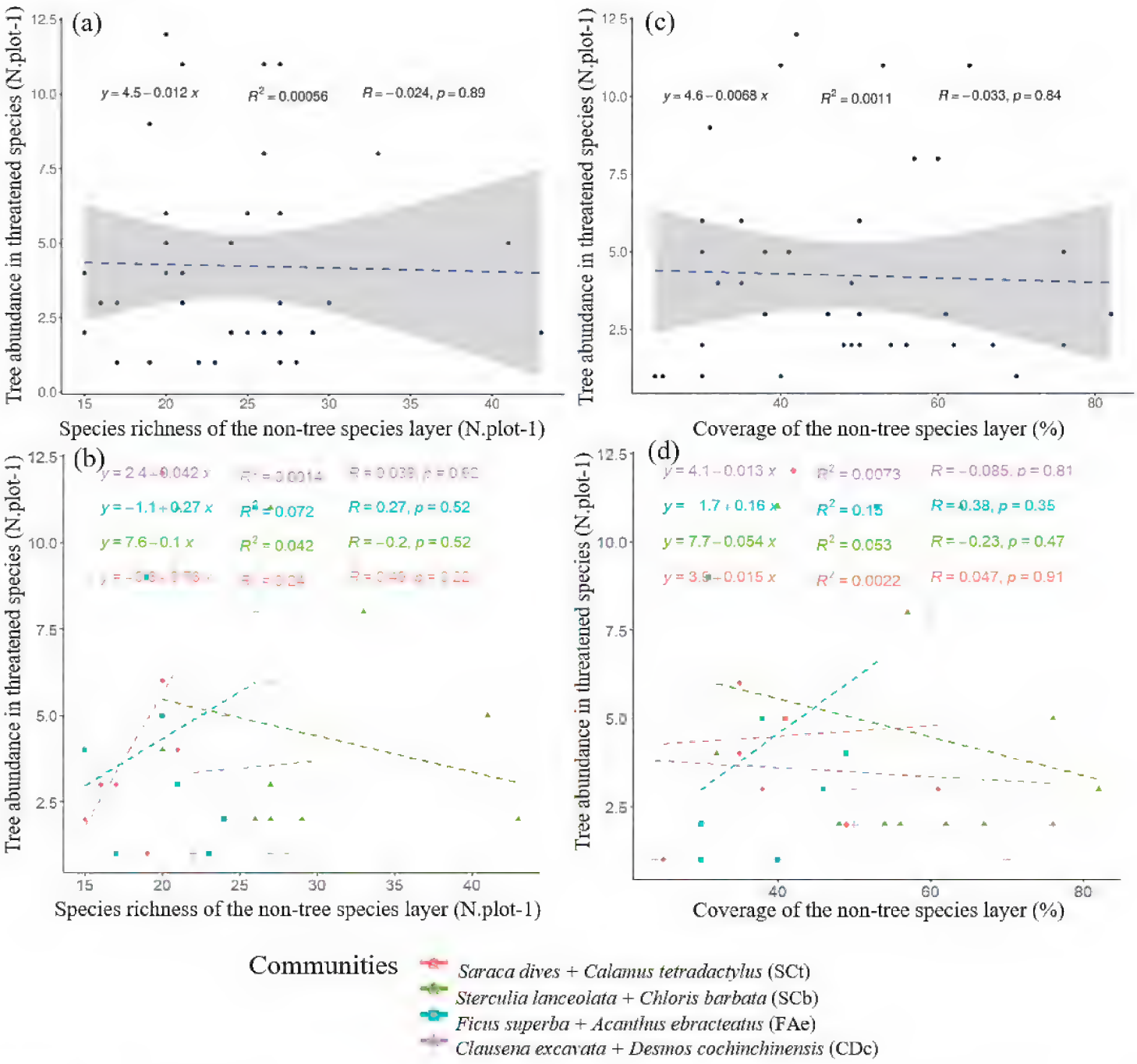

(a)
y = 4.5 − 0.012 x
R² = 0.00056
R = −0.024, p = 0.89
Tree abundance in threatened species (N.plot-1)
Species richness of the non-tree species layer (N.plot-1)
(c)
y = 4.6 − 0.0068 x
R² = 0.0011
R = −0.033, p = 0.84
Coverage of the non-tree species layer (%)
(b)
y = −1.1 + 0.27 x
R² = 0.072
R = 0.27, p = 0.52
y = 7.6 − 0.1 x
R² = 0.042
R = −0.2, p = 0.52
(d)
y = 4.1 − 0.013 x
R² = 0.0073
R = −0.085, p = 0.81
y = 7.7 − 0.054 x
R² = 0.053
R = −0.23, p = 0.47
y = 3.9 − 0.015 x
R² = 0.0022
R = 0.047, p = 0.91
Communities
Saraca dives + Calamus tetradactylus (SCt)
Sterculia lanceolata + Chloris barbata (SCb)
Ficus superba + Acanthus ebracteatus (FAe)
Clausena excavata + Desmos cochinchinensis (CDc)

Figure A4. Linear models of non-tree species and threatened tree species abundance. Graphs (**a**) and (**c**) show the relationship between non-tree species and threatened tree species abundance across communities. Graphs (**b**) and (**d**) present the relationship of non-tree species to threatened tree species abundance separated by the four communities. All relationships are not significant as indicated by the dashed lines. SCt; *Saraca dives* + *Calamus tetradactylus* community. SCb; *Sterculia lanceolata* + *Chloris barbata* community. FAe; *Ficus superba* + *Acanthus ebracteatus* community. CDc; *Clausena excavata* + *Desmos cochinchinensis* community.

Appendix 8

Table A4. Species checklist. This table contains the 302 species which were recorded in the CBNP in course of this study. It includes 153 tree species (comprising the overstorey layer and the regeneration layer) and 149 non-tree species. The classification is provided as well.

No	Species name	Family	Indigenous name	Classification
1	*Acacia lucium* (Benth). I: Nielsen	Mimosaceae	Mán đỉa trâu	Tree
2	*Acanthus ebracteatus* Vahl.	Acanthaceae	Ô rô	Non-tree
3	*Achyranthes aspera* L.	Amaranthaceae	Cỏ xước	Non-tree
4	*Acronychia pedunculata* L.	Rutaceae	Bưởi bung	Tree
5	*Actinodaphne pilosa* (Lour.) Merr.	Lauraceae	Tam tầng	Non-tree
6	*Adenanthera pavonica* L.	Mimosaceae	Muồng ràng ràng	Tree
7	*Aesculus assamica* Griff.	Hippocastanaceae	Kẹn	Non-tree
8	*Aglaia poilanei* Pell.	Meliaceae	Ngâu dại	Non-tree
9	*Aglaia spectabilis* (Miq.) Jain& Bennet. 1987	Meliaceae	Gội nếp	Tree
10	*Aidia pycnantha* (Drake) Tirveng	Rubiaceae	Mãi táp	Tree
11	*Albizia chinensis* (Osbeek) Merr	Fabaceae	Đuôi trâu	Tree
12	*Allophylus livescens* Radlk.	Sapindaceae	Vải đóm	Non-tree
13	*Allospondias lakonensis* (Pierre) Stapf	Anacardiaceae	Dâu da xoan	Tree
14	*Alpinia officinarum* Hance	Zingiberaceae	Riềng ré	Non-tree
15	*Alstonia scholaris* (L.) R.Br.	Apocynaceae	Sữa	Tree
16	*Amomum xanthioides* Wall. ex Baker	Zingiberaceae	Sa nhân núi	Non-tree
17	*Amorphophalus tonkinensis* Engl. & Gehrm.	Araceae	Nưa bắc bộ	Non-tree
18	*Angiopteris evecta* (J.R. Forst.) Hoffm.	Angiopteridaceae	Quan âm tọa liên	Non-tree
19	*Annamocarya sinensis* (Dode) J. Leroy	Juglandaceae	Chò đãi	Tree
20	*Annona glabra* L.	Annonaceae	Na biển	Tree
21	*Antidesma ambiguum* Pax et Hoffm.	Euphobiaceae	Chòi mòi	Non-tree
22	*Aphanamixis polystachya* (Wall.) R. Parke	Meliaceae	Gội gác	Tree
23	*Aporosa macrostachyus* (Tul.) Muell.Arg.	Euphorbiaceae	Tai nghé đuôi to	Tree
24	*Aporusa ficifolia* H. Baillon	Euphorbiaceae	Tai nghé	Tree
25	*Aralia aff. chinensis* L.	Araliaceae	Quầng quầng	Non-tree
26	*Archidendron clypearia*	Fabaceae	Mán đỉa	Tree
27	*Ardisia crenata* Sims	Primulaceae	Trọng đũa	Non-tree
28	*Ardisia gigantifolia* Stapf	Primulaceae	Lá khôi trắng	Non-tree
29	*Ardisia nigropilosa* Pit.	Primulaceae	Trọng đũa lông đen	Non-tree
30	*Ardisia silvestris* Pitard.	Myrsinaceae	Lá khôi tía	Non-tree
31	*Arenga westerhoutii* Griffith	Arecaceae	Búng báng	Non-tree
32	*Artocarpus borneensis* Merr. Subsp. Griffthii (Kurz) Jarr.	Moraceae	Troi	Tree
33	*Asplenium nidus* (L.) J.Sm.	Aspleniaceae	Tổ điểu	Non-tree
34	*Atalantia guillauminii* Sw.	Rutaceae	Quýt hôi	Tree
35	*Averrhea carambola* L.	Oxilidaceae	Khế	Tree
36	*Bambusa blumeana* J. A. & J. H. Schultes	Poaceae	Tre gai	Non-tree
37	*Bambusa chungii* McClure	Poaceae	Dùng phấn	Non-tree
38	*Barringtonia acutangula* (L.) Gaertn.	Lecythidaceae	Lộc vừng lá to	Tree
39	*Bauhinia coccinea* (Lour.) A. DC.	Caesalpiniaceae	Móng bò hoa đỏ	Non-tree
40	*Bauhinia khasiana* var. polystachya (Gagnep.) K.&S.S.Larsen	Caesalpiniaceae	Dây quạch tròn	Non-tree
41	*Bauhinia lakhonensis* Gagnep	Caesalpiniaceae	Dây quạch dẹt	Non-tree
42	*Bauhinia ornata* Kurz	Caesalpiniaceae	Dây móng bò thơm	Non-tree
43	*Begonia aff. wallichinia* A. DC.	Begoniaceae	Thu hải đường vát	Non-tree
44	*Bischofia javanica* Blume (B. trifoliata (Roxb.) Hook. f.)	Euphorbiaceae	Nhội tiết	Tree
45	*Blechnum orientale* L.	Blechnaceae	Quyết lá dừa	Non-tree
46	*Blumea lacineata* (Roxb.) DC.	Asteraceae	Dẻ rách	Non-tree

No	Species name	Family	Indigenous name	Classification
47	*Boehmeria holoseracea* Blume	Urticaceae	Gai rừng	Non-tree
48	*Boehmeria nivea* (L) Gaud	Urticaceae	Lá gai	Non-tree
49	*Bombax malabarica* DC.	Bombacaceae	Gạo rừng	Tree
50	*Breynia fruticosa* (L.) Hook. f.	Euphobiaceae	Bồ cu vẽ	Non-tree
51	*Bridelia balansae* Tutcher	Euphorbiaceae	Đỏm gai	Tree
52	*Bridelia tomntosa* Blume	Euphorbiaceae	Đỏm lông	Tree
53	*Burretiodendron brilletii* (Gagn.) Kost.	Tiliaceae	Kiêng quang	Tree
54	*Bursera tonkinensis* Guillaum	Burseraceae	Rẫm	Tree
55	*Caesalpinia bonduc* (L.) Roxb.	Caesalpiniaceae	Dây móc mèo	Non-tree
56	*Calamus platyacanthus* Warb. Ex Becc.	Arecaceae	Song mật	Non-tree
57	*Calamus tetradactylus* Hance	Arecaceae	Mây	Non-tree
58	*Callicarpa triloba* Lour.	Vitaceae	Chìa vôi	Non-tree
59	*Canarium album*	Burseraceae	Trám trắng	Tree
60	*Canarium subulatum* Guill	Burseraceae	Trám ba cạnh	Tree
61	*Canarium tramdenum* Dai &Yakovl	Burseraceae	Trám đen	Tree
62	*Canthium dicoccum* (Gaertn.) Teysm. & Binn	Rubiaceae	Xương cá	Tree
63	*Carallia brachiata* (Lour.) Merr.	Rhizophoraceae	Trúc tiết	Tree
64	*Carallia diplopetala*	Rhizophoraceae	Răng cá	Tree
65	*Caryota obtusa* Griff.	Arecaceae	Đùng đình	Non-tree
66	*Caryota urens* L.	Palmeae	Móc	Non-tree
67	*Cassia timoriensis* A. DC.	Caesalpiniaceae	Muồng cánh dán	Tree
68	*Castanopsis chinensis* (Spreng.) Hance.	Fagaceae	Dẻ gai	Tree
69	*Castanopsis ferox* (Roxb.) Spach	Fagaceae	Cà ổi vọng phu	Tree
70	*Celastrus hindsii* Benth. & Hook.	Calastraceae	Xạ vàng	Non-tree
71	*Celastrus* sp.	Celastraceae	Xạ đen	Non-tree
72	*Centella asiatica* (L.) Urb.	Apiaceae	Ráu má	Non-tree
73	*Chisocheton paniculatus* Hiern	Meliaceae	Quếch tía	Tree
74	*Chloris barbata* Sw.	Poaceae	Cỏ mật	Non-tree
75	*Chromolaena odorata* (L.) King et Robinson	Asteraceae	Cỏ lào	Non-tree
76	*Chukrasia tabularis* A. Juss.	Meliaceae	Lát hoa	Tree
77	*Cinnamomum ovantum* Allen.	Lauraceae	Rè gừng	Tree
78	*Cissus subtetragona* Blume	Vitaceae	Hồ đằng vuông	Non-tree
79	*Citrus aurantiifolia* (Chritm.) Sw.	Rutaceae	Chanh rừng	Non-tree
80	*Claoxylon indicum* (Reinw.ex Blume)	Euphorbiaceae	Lộc mại	Tree
81	*Clausena excavata* Burm.f.	Rutaceae	Hồng bì rừng	Tree
82	*Cleistanthus myrianthus* (Hassk.) Kurz	Euphobiaceae	Cọc rào	Non-tree
83	*Clerodendrum chinense* (Osk.) Mabb.	Fagaceae	Ngọc nữ thơm	Non-tree
84	*Clerodendrum squamatum* Vahl	Verbenaceae	Xích đồng nam	Non-tree
85	*Cnestis palala* (Lour.) Merr.	Connaraceae	Dây khế	Non-tree
86	*Colocaria gigantea* (Blume ex Hassk) Hook.f.	Araceae	Ráy	Non-tree
87	*Commelina communis* L.	Commelinaceae	Thài lài	Non-tree
88	*Connarus paniculatus* Roxb.	Connaraceae	Dây mấu	Non-tree
89	*Convolvulus parviflorus* Vohl.	Convolvulaceae	Bìm bìm	Non-tree
90	*Cordyline fruticosa* (L.) Goepp.	Asteliaceae	Huyết dụ	Non-tree
91	*Cratoxylon formosum* subsp.prunifolium (Kurz) Gog.	Guttiferae	Đỏ ngọn	Tree
92	*Cratoxylum cochinchinense* (Lour.) Blume	Hypericaceae	Thành ngạnh	Tree
93	*Croton cubiensis* Gagn.	Euphobiaceae	Cù đèn	Non-tree
94	*Cryptocarya lenticellata* Lecomte	Lauraceae	Nanh chuột	Tree
95	*Curculigo gracilis* (Kurz) Wall.	Hyphoxidaceae	Sâm cau	Non-tree
96	*Cyclosorus parasiticus* (L.) Farw.	Thelypteridaceae	Dương xỉ	Non-tree
97	*Cymbidium hybrid*	Orchidaceae	Địa lan	Non-tree
98	*Cymbodium alviclium* sw.	Orchidaceae	Lan kiếm	Non-tree
99	*Desmos cochinchinensis* Lour.	Annonaceae	Dây hoa dẻ	Non-tree
100	*Deutzianthus tonkinensis* Gagnep	Euphorbiaceae	Mọ	Tree

No	Species name	Family	Indigenous name	Classification
101	*Dianella ensifolia* (L.) DC.	Phormiaceae	Hương bài	Non-tree
102	*Dichroa febrifuga* Lour.	Hydrangeaceae	Thường sơn	Non-tree
103	*Dillenia heterosepala* Fin&Gagnep	Dilleniaceae	Lọng bàng	Tree
104	*Dillenia indica* L.	Dilleniaceae	Sổ bà	Tree
105	*Dillenia scabrella* Roxb	Dilleniaceae	Sổ nước	Tree
106	*Dimocarpus fumatus* subsp. indochinensis Leenh	Sapindaceae	Nhãn rừng	Tree
107	*Dioscorea alata* L	Dioscoreaceae	Củ mỡ	Non-tree
108	*Dioscorea persimilis* Prain et Burk.	Dioscoreaceae	Củ mài	Non-tree
109	*Diospyros decandra* Lour	Ebenaceae	Nhọ nồi	Tree
110	*Diospyros petelotii* Merr.	Ebenaceae	Thị mấm	Tree
111	*Diospyros pilosula* (A. DC.) Hiern	Ebenaceae	Thị rừng	Tree
112	*Diospyros susarticulata* Lec,	Ebenaceae	Thị đốt cao	Tree
113	*Donella lanceolata* (Bl.) Aubr.	Sapotaceae	Sạp đỏ	Non-tree
114	*Dracaena sanderiana* forma virescens Hort.	Dracaenaceae	Sống đời	Non-tree
115	*Dracontomelon duperreanum* Piere	Anacardiaceae	Sấu	Tree
116	*Drimycarpus racemosus* Hook.	Anacardiaceae	Sơn xã	Tree
117	*Drynaria fortunei* (Merr.) J.Sm.	Polypodiaceae	Bổ cốt toái	Non-tree
118	*Duabanga grandiflora* (DC.) Walp.	Sonneratiaceae	Phay sừng	Tree
119	*Elaeagnus bonii* Lecomte	Elaeagnaceae	Nhót rừng	Non-tree
120	*Elaeocarpus griffithii* (Wight) A. Gray	Elaeocarpaceae	Côm tầng	Tree
121	*Elephantopus mollis* H.B.K.	Asteraceae	Chân voi	Non-tree
122	*Eleusine indica* (L.) Gaertn.	Poaceae	Cỏ mần trầu	Non-tree
123	*Embelia laeta* (L.) Mez.	Myrsinaceae	Rè vũ	Non-tree
124	*Endospermum chinense* Benth.	Euphorbiaceae	Vạng trứng	Tree
125	*Engelhardtia roxburghiana* Wall	Juglandaceae	Chẹo tía	Tree
126	*Entada glandulosa* Pierre ex Gagn.	Mimosoideae	Bàm bàm tuyến	Non-tree
127	*Eriobotrya bengalensis* (Roxb.) Hook.f.	Rosaceae	Tỳ bà rừng	Tree
128	*Erythrophleum fordii* Oliv.	Caesalpiniaceae	Lim xanh	Tree
129	*Euodia lepta* (Spreng) Merr.	Rutaceae	Chè đắng	Tree
130	*Eurya ciliata* Merr.	Theaceae	Súm lông	Tree
131	*Eurycoma longifolia* Jack.	Simaroubaceae	Bền bệt	Non-tree
132	*Excoecaria cochinchinensis* var. viridis (Pax & Hoffm.)Merr.	Euphobiaceae	Sơn đề	Non-tree
133	*Ficus alongensis* Gagnep	Moraceae	Sung hạ long	Tree
134	*Ficus altissima* Blume	Moraceae	Đa trâu	Tree
135	*Ficus annulata* Blume	Moraceae	Đa nhộng vàng	Tree
136	*Ficus auriculata* Lour.	Moraceae	Vả	Tree
137	*Ficus capillipes* Gagn.	Moraceae	Đa cuống bẹt	Tree
138	*Ficus chlorocarpa* Benth.	Moraceae	Sung rừng	Tree
139	*Ficus hirta* Vahl	Moraceae	Vú bò	Non-tree
140	*Ficus hispida* L.f.	Moraceae	Ngái	Tree
141	*Ficus retusa* L.	Moraceae	Si	Tree
142	*Ficus rumphii* Bl.	Moraceae	Da bò	Tree
143	*Ficus superba* var.japonica Miq.	Moraceae	Sộp	Tree
144	*Garcinia cochinchinesis* (Lour.) Choisy	Clusiaceae	Bứa tai chua	Tree
145	*Garcinia cowa* Roxb. ex DC.	Clusiaceae	Tai chua	Tree
146	*Garcinia oblongifolia* Champ.	Clusiaceae	Bứa	Tree
147	*Garcinia tinctoria* (DC.) W. Wight	Clusiaceae	Bứa cơm	Tree
148	*Garruga pinnata* Roxb.	Burseraceae	Trám mao	Tree
149	*Gelsemium elegans*	Gelsemiaceae	Dây lá ngón	Non-tree
150	*Gigantochloa albo-ciliata* (Munro) Kurz	Poaceae	Le	Non-tree
151	*Gironniera subequalis* Planch.	Ulmaceae	Ngát	Tree
152	*Gleichenia linearis* Clarke	Gleicheniaceae	Ràng ràng	Non-tree
153	*Glochidion hirsutum* (Roxb.) Voigt	Euphorbiaceae	Bọt ếch biển	Tree
154	*Glycosmis cymosa* (Pierre) Stone	Rutaceae	Màu cau đá	Tree

No	Species name	Family	Indigenous name	Classification
155	*Gnetum montanum*	Gnetaceae	Dây gắm	Non-tree
156	*Gomphandra tonkinensis* Gapnep	Icacinaceae	Bổ béo	Non-tree
157	*Goniothalamus macrocalyx* Ban	Annonaceae	Màu cau trắng	Tree
158	*Gynostemma pentaphyllum*	Cucurbitaceae	Giảo cổ lam	Non-tree
159	*Helicteres angustifolia* L.	Strerculiaceae	Tổ kén tròn	Non-tree
160	*Helicteres hirsuta* Lour	Malvaceae	Thao kén cái	Non-tree
161	*Helixanthera parasitica* Lour.	Loranthaceae	Tầm gửi ký sinh	Non-tree
162	*Heterosmilax gaudichaudiana* (Kunth.) Maxim	Smilacaceae	Khúc khắc	Non-tree
163	*Hydnocarpus hainanensis* (Merr.) Sleum.	Flacourtiaceae	Nang trứng hải nam	Tree
164	*Iodes cirrhosa* Turez	Icacinaceae	Mộc thông	Non-tree
165	*Ixora umbellata* Vahl	Rubiaceae	Đơn ớt	Non-tree
166	*Jasminum subtriplinerve*	Oleaceae	Chè vằng	Non-tree
167	*Knenma conferta* Warb.	Myristicaceae	Máu chó	Tree
168	*Lagerstroemia calyculata* Kurz	Lythraceae	Săng lẻ	Tree
169	*Lemmaphyllum microphyllum* Presl.	Polypodiaceae	Tắc kè đá	Non-tree
170	*Lilium brownii* F.E Brown var colchesteri Wilson	Liliaceae	Tỏi rừng	Non-tree
171	*Liquidambar formosana* Hance	Hamamelidaceae	Sau sau	Tree
172	*Lithocarpus fissus* Champ. ex benth	Fabaceae	Sồi phảng	Tree
173	*Lithocarpus hemisphaericus* (Drake) Barnett	Fagaceae	Trâm dày	Tree
174	*Litsea monopetala* (Roxb.) Pers.	Lauraceae	Mò giấy	Tree
175	*Litsea verticillata* Hance	Lauraceae	Bời lời vòng	Tree
176	*Livistona halongensis* T.H. Nguyen & Kiew	Arecaceae	Cọ hạ long	Tree
177	*Lonicera japonica* Thunb.	Caprifoliaceae	Kim ngân	Non-tree
178	*Lycopodiella cernua* (L.) Franco & Vasc.	Arecaceae	Thông đất	Non-tree
179	*Lygodium japonicum* Sw	Lygodiaceae	Bòng bong	Non-tree
180	*Macaranga denticulata* (Blume) Muell. Arg.	Euphorbiaceae	Lá nến	Tree
181	*Machilus bonii* Lecomte	Lauraceae	Kháo vàng	Tree
182	*Machilus salicina* Hance	Lauraceae	Kháo lá liễu	Tree
183	*Machilus thunbergii* Sieb. & Zucc.	Lauraceae	Rè thunberg	Tree
184	*Machilus velutina* Champ. ex Benth.	Lauraceae	Kháo lông	Tree
185	*Maclura cochinchinensis* (Lour.)	Moraceae	Mỏ quạ	Non-tree
186	*Maesa balansae* Mez.	Myrsinaceae	Đơn nem	Non-tree
187	*Maesa montana* A.DC.	Myrsinaceae	Đơn độc trắng	Non-tree
188	*Maesa ramentacea* Wall.	Myrsinaceae	Đơn độc đỏ	Non-tree
189	*Magnolia balansae*	Magnoliaceae	Giổi bà	Tree
190	*Malaisia scandens* (Lour.) Pl.	Moraceae	Duối leo	Non-tree
191	*Mallotus apelta* (Lour.) Muell.-Arg.	Euphorbiaceae	Ba bét trắng	Non-tree
192	*Mallotus cochinchinensis* Lour.	Euphorbiaceae	Ba soi	Tree
193	*Mallotus philippensis* (Lamk.) Muell.-Arg.	Euphobiaceae	Cánh kiến	Non-tree
194	*Mangifera longipes* Griff.	Anacardiaceae	Trôi	Tree
195	*Manglietia rufibarbata* Dandy	Magnoliaceae	Giổi xanh	Tree
196	*Markhamia cauda-felina* (Hance) Craib.	Bignoniaceae	Kè đuôi nhông	Tree
197	*Melaleuca cajuputi* Powell	Myrtaceae	Tràm nước	Tree
198	*Melodinus annamensis* Pit.	Apocynaceae	Dây rom sữa	Non-tree
199	*Memecylon edule* Roxb.	Melastomataceae	Sầm sì	Tree
200	*Mesua ferrea* L.	Clusiaceae	Vắp	Tree
201	*Microcos paniculata* Miq	Tiliaceae	Mé cò ke	Tree
202	*Microsorum hancockii* (Bak.) Ching.	Polypodiaceae	Lá han	Non-tree
203	*Millettia pulchra* Kunz	Fabaceae	Nam bạch chỉ	Non-tree
204	*Millettia sp*	Papilionoideae	Kè	Tree
205	*Morinda citrifolia* L.var.bracteata Hook.f.	Rubiaceae	Nhàu	Tree
206	*Murraya glabra* (Guillaum.)	Rutaceae	Vương tùng	Tree
207	*Musa paradisiaca* L.	Musaceae	Chuối rừng	Non-tree

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208	*Mussaenda crosa* Champ. ex Benth.	Rubiaceae	Bướm bạc môn	Non-tree
209	*Mussaenda pilosissima* Val.	Rubiaceae	Dây bướm lông	Non-tree
210	*Nervilia fordii* (Hance) Sch.	Orchidaceae	Lan một lá	Non-tree
211	*Paliorus tonkinensis* Pit.	Rhamnaceae	Táo dáng	Tree
212	*Pandanus tectorius* Sol ex Park.	Pandanaceae	Dứa dại	Non-tree
213	*Paramichelia baillonii* (Pierre) Hu	Magnoliaceae	Giổi găng	Tree
214	*Pavetta indica* L.	Rubiaceae	Cẳng gà	Tree
215	*Peltophorum pterocarpum*	Caesalpiniaceae	Lim xẹt	Tree
216	*Persea balansae* Airy-Shaw	Lauraceae	Kháo lá to	Tree
217	*Persea mollis* (W.W.Sm.) Kost.	Lauraceae	Kháo tai trâu	Tree
218	*Pheobe tavoyana* Meisn.	Lauraceae	Sụ lá to	Tree
219	*Phoebe pallida* Nees.	Lauraceae	Kháo nước	Tree
220	*Phrynium placentarium* (Lour.) Merr.	Maranthaceae	Lá dong	Non-tree
221	*Phyllanthus reticulatus* Poir.	Euphobiaceae	Phèn đen	Non-tree
222	*Phytele phantoideae*	Arecaceae	Xuôi	Non-tree
223	*Piper chaudocanum* C. DC	Piperaceae	Trầu rừng	Non-tree
224	*Piper lolot* C. DC.	Piperaceae	Lá lốt	Non-tree
225	*Podocarpus fleuryi* Hickel	Podocarpaceae	Kim giao	Tree
226	*Portulaca oleacea* L.	Portulacaceae	Sam núi đá	Non-tree
227	*Psychotria montana* Blume	Rubiaceae	Lấu	Non-tree
228	*Pteris vittata* L.	Pteridaceae	Chân rết	Non-tree
229	*Pterospermum diversifolium*	Sterculiaceae	Lòng mang lá đa dạng	Tree
230	*Pterospermum heterophyllum* Hance	Sterculiaceae	Lòng mang xanh	Tree
231	*Pterospermum truncatolobatum* Gagn.	Sterculiaceae	Lòng mang cụt	Tree
232	*Quercus platycalyx* Hickel & A. Camus	Fabaceae	Sồi đĩa	Tree
233	*Quisqulis indica* L.	Combretaceae	Dây dầu giun	Non-tree
234	*Randia dasycarpa* (Kurz) Bakh. f	Rubiaceae	Găng nhung	Non-tree
235	*Rauvolfia cambodiana* Pierre ex Pit.	Apocynaceae	Ba gạc	Non-tree
236	*Rauvolfia verticillata* (Lour.) Baill.	Apocynaceae	Ba gạc vòng	Non-tree
237	*Rhapis micrantha* Becc	Arecaceae	Lụi	Non-tree
238	*Rhizophora apiculata* Bl.	Rhizophoraceae	Đước đôi	Tree
239	*Rhodoleia championii* Hook.	Hamamelidaceae	Hồng quang	Non-tree
240	*Rhus chinensis* Muell.	Anacardiaceae	Dâu dắt	Tree
241	*Rinorea bengalensis* (Wall.) Kuntze	Violaceae	Ngát giả	Tree
242	*Sapium discolor* (Champ. ex Benth.) Muell.-Arg.	Euphorbiaceae	Sòi tía	Tree
243	*Saraca dives*	Fabaceae	Vàng anh	Tree
244	*Sargentodoxa cuneata* (Oliv.) Rehd. et Wiis.	Sargeniodoxceae	Huyết đằng	Non-tree
245	*Sauropus androgynus* (L.) Merr	Euphobiaceae	Rau ngót rừng	Non-tree
246	*Sauropus macranthus* Hassk.	Euphorbiaceae	Vỏ rộp	Non-tree
247	*Schefflera alongensis* R.Vig.	Araliaceae	Chân chim hạ long	Non-tree
248	*Schefflera heptaphylla* (L.) Frodin	Araliaceae	Chân chim tám lá	Non-tree
249	*Schizostachyum dulloa*	Poaceae	Nứa tép	Non-tree
250	*Secamone elliptica* R.Br.	Asclepiadaceae	Ro bầu dục	Non-tree
251	*Selaginella decipiens* Warb.	Selaginellaceae	Quyển bá	Non-tree
252	*Selaginella delicatula* (Desv.) Alst.	Selaginellaceae	Quyển bá mỏng	Non-tree
253	*Sindora tonkinensis* A. Chev. ex K. S. Larsen	Caesalpiniaceae	Gụ lau	Tree
254	*Sinosideroxylon racemosum* (Dub.) Aubr.	Sapotaceae	Mai lai	Tree
255	*Sloanea* sp.	Elaeocarpaceae	Côm nhím	Tree
256	sp. 1	Moraceae	Đèo heo	Tree
257	sp. 2	Euphorbiaceae	Mấy	Tree
258	sp. 3	Rubiaceae	Đèn en	Tree
259	sp. 4	sp4	Áng nước	Tree

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260	sp. 5	sp5	Vấp	Tree
261	*Spilanthes paniculata* Wall. ex DC	Asteraceae	Cây cúc áo	Non-tree
262	*Sporobolus fertilis* (Steud.) Calayton	Poaceae	Cỏ lông công	Non-tree
263	*Stephania rotunda* Lour.	Menispermaceae	Bình vôi	Non-tree
264	*Sterculia foetida* L.	Sterculiaceae	Mần lái	Tree
265	*Sterculia lanceolata* Cav.	Sterculiaceae	Sảng nhung	Tree
266	*Streblus asper* Lour.	Moraceae	Ruối nhám	Non-tree
267	*Streblus laxiflos* (Hutch.) Corner	Moraceae	Duối rừng	Tree
268	*Streblus macrophyllus* Bl.	Moraceae	Mạy tèo	Tree
269	*Streblus tonkinensis* (Dub. & Eberh.) Corner	Moraceae	Teo nông	Tree
270	*Strychnos angustiflora* Benth.	Loganiacaea	Củ chấy	Non-tree
271	*Strychnos wallichii* Steud. = S. gaulthierana Pierre	Loganiacaea	Mã tiền dây	Non-tree
272	*Swietenia macrophylla*	Meliaceae	Dái ngựa	Tree
273	*Symplocos laurina* var. acuminata (Miq) Brand.	Symplocaceae	Dung giấy	Tree
274	*Syzygium bullockii* (Hance) Merr. et Perry	Myrtaceae	Trâm voi	Tree
275	*Syzygium jambos* (L.) Alston	Myrtaceae	Roi rừng	Tree
276	*Syzygium pachysarcum* (Gagn.) Merr. & Perry.	Myrtaceae	Trâm sánh	Tree
277	*Syzygium wightianum* Wight et Arn.	Myrtaceae	Trâm trắng	Tree
278	*Syzygium zeylanicum* (L.) DC.	Myrtaceae	Trâm vỏ đỏ	Tree
279	*Syzysium senamangense* (Bl.) Merr. & Perry.	Myrtaceae	Mận rừng	Tree
280	*Taractogenos sp*	Flacourtiaceae	Chùm bao	Tree
281	*Taxillus chinensis* (DC.) Dans.	Loranthaceae	Hồng tuyến	Non-tree
282	*Tetracera scandens* (L.) Merr	Dilleniaceae	Dây chặc chìu	Non-tree
283	*Tetrastigma retinervum* Planch.	Vitaceae	Dây doãn	Non-tree
284	*Thunbergia eberhardtii* R.Ben.	Acanthaceae	Cát đằng vàng	Non-tree
285	*Tinospora sagitta* (Oliv.) Gagnep	Menispermaceae	Củ gió	Non-tree
286	*Tinospora sinensis* (Lour.) Merr.	Menispermaceae	Đơn xương	Non-tree
287	*Triumfetta bartramia* L.	Tiliaceae	Ké	Non-tree
288	*Tsoongiodendron odorum* Chun	Magnoliaceae	Giổi lụa	Tree
289	*Uvaria microcarpa* Champ. ex Benth.	Annonaceae	Dất lông	Non-tree
290	*Ventilago leiocarpa* Benth.	Rhamnaceae	Dây cốt khí	Non-tree
291	*Verbesina biflora* L	Asteraceae	Lá mui biển	Non-tree
292	*Vernonia aff. acumingiana* Benth.	Asteraceae	Thuốc máu	Non-tree
293	*Vitis balanseana* Blume	Vitaceae	Đậu xương	Non-tree
294	*Vittaria ensiformis* Sw.	Thelypteridaceae	Quyết dương xỉ	Non-tree
295	*Wendlandia paniculata* (Roxb.) DC.	Rubiaceae	Hoắc quang trắng	Tree
296	*Wrightia tomentosa* (Roxb.) Roem. & Schult.	Apocynaceae	Thừng mực	Tree
297	*Wrightia laevis* Hook.f.	Apocynaceae	Thừng mực mỡ	Tree
298	*Xerospermum noronhianum* Blume.	Sapindaceae	Vải rừng	Tree
299	*Zanthoxylum nitidum* (Lamk.) DC.	Rutaceae	Sẻn gai	Tree
300	*Zephyranthes carinata* Herb	Amaryllidaceae	Tóc tiên	Non-tree
301	*Zizyphus eonoplia* (L) Mill.	Rhamnaceae	Táo rừng	Tree
302	*Zizyphus incurva* Roxb.	Rhamnaceae	Táo vòng	Tree